COMPARATIVE SEED AND REGENERATION BIOLOGY OF TWO THATCHING REED SPECIES (*THAMNOCHORTUS INSIGNIS AND T. ERECTUS*, RESTIONACEAE)

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SUMMARY

The effect of harvesting on the seed and seedling ecology and the effect of fire and harvesting on the population dynamics of two thatching reed species, namely *Thamnochortus insignis* and *Thamnochortus erectus* were studied. The study species are both perennial hemicryptophytes each with a different regeneration mode, the former being a non-sprouter and the latter a resprouter. Despite being increasingly harvested in the agriculturally marginal areas of the southern Cape coast, no information exists on population dynamics and population processes that depend on the distribution and behaviour of seeds. Furthermore, Restionaceae which are physiognomically and floristically characteristic of the fynbos have generally been poorly studied. Thus, this study aimed to increase our understanding of the effect of harvesting on the seed bank dynamics and the effect of fire and harvesting on population dynamics of these species, as well as to provide managers of thatch stands with guidelines for the sustainable utilization of the resource. Seed bank dynamics and response of the species to disturbance were the focus of this study, but were placed in the context of their whole life cycles.

Soil seed bank densities of both species were high; with that of *T. insignis* being approximately two times larger than that of *T. erectus*. This was attributed to greater seed production of *T. insignis* compared to *T. erectus*, rather than to longer survival of seed in the soil. Both species produced considerably more seeds than were incorporated into the seed bank and it was during this life history stage that the largest seed losses were observed. The seed bank densities of both species were distinctly seasonal, with direct seed counts for *T. insignis* varying between 1633 ± 2601 (mean ± standard deviation) seeds per m^2 before dispersal and 3773 ± 6027 seeds per m^2 after dispersal. Seed counts for *T. erectus* varied between 1134 ± 2644 seeds per m^2 before dispersal and 2530 ± 3482 seeds per m^2 after dispersal. Seed bank estimates from germination were lower. Annual seed production and seed bank densities of both species showed large inter-annual variations, as well

as differences between species. Harvesting resulted in a drastic decline in both seed production and post-dispersal seed bank density. Active dispersal of seed during harvesting resulted in an increase in pre-dispersal seed bank density. Both species have seasonally persistent seed banks, and seed losses over the year following seed input were moderate. An accumulation of seeds in the soil over the two years was observed for both species. Seed burial showed that seed persistence and losses in seed banks differed between species and experimental seed bank type. *Thamnochortus erectus* showed greater seed persistence and *T. insignis* showed greater seed losses. These results conflict with actual observations of seed bank densities. Burial bags showed greater seed persistence and burial boxes showed greater seed losses for both species. Recruitment and seedling survival in mature vegetation was limited for both species, although *T. insignis* appeared to have more potential than *T. erectus* for recruitment in this environment. In contrast, *T. insignis* seedling recruitment was massive in the post-disturbance environment, indicating that the dormancy breaking cue may be mediated through increased resources in the disturbed environment. Moreover, germination appears to be cued by fire, although post-fire recruitment was not confined to the first germination season after fire. *Thamnochortus erectus* seedling density was variable after disturbance and showed no large differences in the post-disturbance environment compared to mature vegetation, indicating that germination was not stimulated by environmental stimuli in the post-disturbance environment. The "open" microhabitat was favoured by seedlings of both species.

Fire appeared to have a greater impact than harvesting on the population structure of both species. Culm production and resumption of seed production was rapid for both species, although reproductive output was both larger and increased more rapidly with time for *T. insignis* compared to *T. erectus*. A single disturbance event increases the successful establishment of the non-sprouter, *T. insignis*, largely by massive seedling recruitment, although many plants survive and resprout from a subterranean base after harvesting. Population expansion of *T. erectus* after

fire is probable, although not after harvesting. This was largely due to the ability of the resprouter, *T. erectus*, to maintain population size by adult plant survival and vegetative growth after a disturbance event, as well as recruiting seedlings. *Thamnochortus insignis* can, thus, be seen as a pioneer species and *T. erectus* can be seen as a persistent species.

This study contributes to the understanding of soil seed bank dynamics in fynbos and is the first comprehensive study of the seed and seedling biology of African Restionaceae. The implications of these results for commercial harvesting of the study species are discussed.

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CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

1.1 THESIS RATIONALE

The harvesting of thatch has become an increasingly important veld-based industry in the agriculturally marginal areas of the southern Cape coast. In addition to periodic fires, brushcutting has therefore become a major disturbance factor in restioid fynbos types of the Cape lowlands (Bond 1984, Kruger and Bigalke 1984, Cowling *et al.* 1987b, Ball 1991). In order to manage this resource on a sustainable basis, information is required on the dynamics of the principle thatch species, *Thamnochortus insignis* Masters and *Thamnochortus erectus* (Thunb.) Masters. Both species are rush-like, aphyllous, evergreen, hemicryptophytes belonging to the family Restionaceae.

Many authors have commented on the general lack of documentation on the population dynamics and ecology of South African Restionaceae, a family physiognomically and floristically characteristic of the fynbos (Milewski and Esterhuysen 1977, Linder 1985, 1991). The dynamics of seed banks are particularly important as they ultimately guarantee the ability of populations of species to survive potentially destructive biotic and abiotic events (Templeton and Levin 1979, Thompson and Grime 1979, Keddy *et al.* 1989). Previous population studies have gained valuable insights into the dynamics of shrubland communities. Canopy-stored seed banks have been studied in detail in mediterranean-type ecosystems, including fynbos (e.g. Bond *et al.* 1984, Bond 1985, Bond *et al.* 1995, Cowling *et al.* 1987a, Midgley 1989, Lamont *et al.* 1991, Pannell and Myerscough 1993, Van Wilgen and Viviers 1985). Soil-stored seed banks, especially those of shrubs, have been fairly well studied in other fire-prone vegetation types (e.g. Keeley 1977, 1987; Mallik *et al.* 1984, Auld 1986, Willems 1988, Zammit and Zedler 1988, 1994; Meney *et al.* 1994). Research on soil seed banks in fynbos has centered on the seed and seedling ecology of shrubs of the Proteaceae, Ericaceae, Rhamnaceae, Thymelaeaceae, Rutaceae, Asteraceae and Polygalaceae (e.g. Kilian and Cowling 1992, Le Maitre 1988, Pierce and Cowling 1991a, 1991b; Manders 1990, Musil 1991). Thus, although, soil-

stored seed banks in fynbos shrubs have been reasonably well studied there is a major gap in our knowledge with respect to the seed biology and, more specifically, the seed bank ecology of the restioid component of the vegetation type. The only research carried out thus far on Restionaceae has been by Musil (1991) on *Thamnochortus punctatus*, a South African species and Meney *et al.* (1994) on southwestern Australian species that grow in kwongan, a vegetation type very similar to fynbos.

The study was, therefore, initiated to address the lack of knowledge of the seed bank ecology of the principle thatch species and to provide managers of thatch stands with guidelines for the sustainable utilization of the resource. Knowledge of the communities and species concerned and a general interest in the thatching reed industry, gained during previous studies was useful. A limited study by Singleton (1991) on the seed bank dynamics of *T. insignis* emphasized the gap in the knowledge on Cape fynbos seed bank ecology and highlighted the need for a more detailed study. The study formed part of a wider collaborative study by the Botany Department at the University of Cape Town and the National Botanical Institute funded by the Department of Agriculture which aims to develop an understanding of the biology of thatch and to use this knowledge to develop guidelines for the improved production of thatch (Linder *et al.* 1992, Davis 1993).

In the fire-prone fynbos shrublands, the survival and expansion of plant populations is dependent on their ability to regenerate after disturbance. Thus, as is the case in other mediterranean shrublands, fire is one of the most important selective agents in the evolution of life history traits beacuse it creates open space and increases the availability of resources for recruitment (Naveh 1975, Gill 1981, Christensen 1985, Cowling 1987). Fynbos species posses a wide array of reproductive traits (e.g. ability to resprout, fire stimulated seed release, seed germination and flowering) that enable population maintenance in the face of recurrent fire (Kruger 1983, Le Maitre and Midgley 1992). An understanding of the responses of species or trait-complexes (e.g. non-sprouting and serotiny) in relation to varying

components of the fynbos fire regime, provide the predictive basis for improved management capability. Our knowledge about the interaction of life history traits with seed bank dynamics and post-fire seedling establishment is very scant. Life history studies of individual species provide the basis for understanding the underlying patterns in seed bank and vegetation dynamics.

This study investigated the seed characteristics, population structure, seed production, soil seed bank dynamics and seedling establishment of the two principle thatch species, before and after harvesting. The primary objective was to examine factors influencing seed bank dynamics. The general processes influencing inputs and losses from the seed bank were studied, including predation, dormancy/germination mechanisms and seed decay. A more limited aspect of this study, focussed on the effect of fire and harvesting on the population dynamics of both species.

The importance of population level studies has been emphasized as a requirement for gaining a predictive understanding of fynbos community dynamics (Manders and Cunliffe 1987). Many authors have encouraged the integrated and comprehensive study of the life histories of plants, as opposed to isolated studies of one or a few components only (e.g. Harper and White 1974, Auld 1987, Price and Jenkins 1987, Parker *et al.* 1989). In this study, the seed and seedling ecology of the two species are placed in the context of whole life cycles of the plants. It thus provides comparative insights into the biology of the two allopatric and closely related congeners (Linder 1991). It is the first comprehensive study on the reproductive biology of African Restionaceae.

1.2 SPECIFIC AIMS

1.2.1 SEED BANKS

The existence and importance of the soil seed banks have been recognized since Darwin's time (Darwin 1859), although they have only been widely studied over the past two decades (e.g. Heydecker 1973, Harper 1977, Thompson and Grime 1979, Fenner 1985). For many decades, the literature on seed banks was a collection of fragmented and unrelated studies, representing a multitude of approaches, goals and methodological defects (Leck *et al.* 1989). Only recently, has a distinctive literature on both the nature and dynamics, and on the methodology, for seed bank studies emerged. As a result, a number of comprehensive reviews on the subject have been written (e.g. Cook 1980, Roberts 1981, Leck *et al.* 1989, Warr *et al.* 1993).

The study species differ in their regenerative responses to disturbance, such as fire or harvesting. *Thamnochortus insignis* and *T. erectus* are classified as a non-sprouter and a resprouter, respectively (Keeley 1981). Non-sprouters are killed by fire and are dependent exclusively on seed produced in years between disturbance events for their regeneration and population survival. These species are reliant on the availability of soil-stored seed or a large annual seed production to enable population expansion after fire. Fires in populations that have yet to establish a seed bank, can bring about local extinction of fire-sensitive species (Bradstock and Myerscough 1981, Van Wilgen 1981). Resprouters are rarely killed by fire and regenerate vegetatively (for example from buds that occur on subterranean organs), although regeneration is also possible by soil-stored seed. Species able to resprout after fire, require only sufficient seed to offset mortality of parent plants. Populations could be expected to decline only if senescent individuals are not replaced by new genets in the long term (Bradstock and Myerscough 1988). The dynamics of seed banks are thus important as they ultimately guarantee the maintenance of populations of non-sprouters

(Parker *et al.* 1989), as well as contributing to inter-fire recruitment during periods of low seed production or high seed mortality.

This study aimed to determine the size and seasonal persistence of the seed banks of *T. insignis* and *T. erectus* each with their different regeneration modes. In all mediterranean shrublands reproduction between fires is limited by a variety of factors (Kruger 1983, Keeley 1986). Thus, there is a strong selection for persistent seed banks in order to maximize recruitment in open, nutrient-rich, low predation environments after fire (Givinish 1981, Lamont *et al.* 1991). Persistent seed banks are selected when maintenance of the population through periods of risk is important (Parker *et al.* 1989). In fynbos, fire has the potential to be disastrous for non-sprouter plants during seasons of low seed production as recruitment after fire is dependent on seed. In contrast, fire rarely has the potential to be disastrous for resprouter plants; such as during a very intense fire. Thus, one would expect the non-sprouter, *T. insignis* to have a seasonally persistent seed bank in order to protect against the risk of fire. One would expect the resprouter, *T. erectus*, whose plants are rarely killed by fire and are extremely long-lived to be less reliant on the seed fraction, and consequently have a weakly persistent or transient seed bank.

During its life cycle an organism has a finite amount of resources available to it. Natural selection results in each organism optimizing the partitioning of these resources to maximize fitness. The relative allocations between the various demands will vary between organisms in different habitats, and allocation of a large quantity of resources to one activity can only be made at the expense of others. In a frequently disturbed habitat, the ability to produce numerous offspring is a more important component of fitness than vegetative growth. In contrast, the ability to compete successfully with neighbouring plants is more important in habitats that are not frequently disturbed, as mortality tends to be density dependent. In these environments, the allocation of a larger proportion of resources to vegetative expansion to compete successfully with neighbours may be the best strategy

to maximise reproduction in the long-term. Fire recurrence intervals (i.e. disturbance) are more frequent in *T. insignis* communities than in *T. erectus* communities. Since the nonsprouter, *T. insignis*, is entirely dependent upon seedling establishment after fire, one would expect a large proportion of its energy to be allocated to sexual reproduction (i.e. seed production) (Keeley and Keeley 1977). In the resprouter, *T. erectus*, resprouting following fire is very succesful, thus, one would expect that the majority of resources would not be allocated to sexual reproduction but to vegetative expansion (i.e. maintainence of a large bud bank) (Keeley and Keeley 1977). Both the cost of maintainence of dormant buds (Midgley 1987, Meney and Dixon 1988, Pate *et al.* 1991, Stock *et al.* 1987) and seed production (Stock *et al.* 1990) are high. In both species there, thus, exists a trade-off between the ability to expand vegetatively and produce large quantities of seed (Lamont and Barret 1988). Thus, one would expect that *T. insignis* has a poor ability to expand vegetatively and that *T. erectus* has a small annual seed production.

1.2.2 LIFE CYCLE DYNAMICS

A life cycle of a plant is defined as: "the developmental changes undergone by the individuals comprising a population, including fertilization, reproduction and the death of those individuals, and their replacement by a new generation" (Allaby 1992). Life cycles are linear in respect to individuals but cyclical with respect to populations. These stages may be divided into the following processes: (1) seed production, (2) seed dispersal, (3) seed storage, (4) germination, (5) seedling establishment, and (6) development of seedling to adult. The life history traits of the non-sprouter *T. insignis* and the resprouter *T. erectus* were compared, and related to their regenerative modes. For each species, seed production and subsequent seed (pre- and post-dispersal, decay and germination) and seedling losses through the life cycle were quantified for two consecutive years at one study site. In fynbos recruitment of most species is thought to be limited to the first year after fire (Kruger 1979, 1984). The emergence and survival of seedlings of both

study species were monitored in mature vegetation to determine whether the species had potential to recruit in undisturbed vegetation. The study attempted to establish the processes limiting population recruitment after harvesting.

1.2.3 THE EFFECTS OF DISTURBANCE (FIRE AND HARVESTING) ON PLANT MORTALITY, VEGETATIVE REGROWTH AND SEEDLING RECRUITMENT

Despite the commercial importance of thatching reed no data exists on the effects of disturbance (fire and harvesting i.e. defoliation) on the principal thatching reed species. Yet, knowledge of these factors is necessary if these resources are to be managed on a sustainable basis. I compared the effect of fire and harvesting on plant mortality, vegetative regrowth and seedling recruitment of the two study species. The study aimed to quantify and compare adult plant mortality and survival in the two study species, and determine whether any sex or size class was more vulnerable to mortality after disturbance. It was postulated that disturbance would result in minimal mortality of adult plants of the resprouter plants, compared to the non-sprouter. It was also postulated that the rate of culm and seed production would be higher in the resprouter species after disturbance. This study aimed to quantify and compare vegetative regrowth and seed production, and to determine whether any pattern in culm regrowth exists in the two study species after fire and harvesting. Many species depend almost entirely on disturbance events to stimulate germination of seed (Keeley 1991). Although seedling recruitment has been observed for both species in undisturbed vegetation, large recruitment events have been observed in disturbed vegetation for *T. insignis*. The study aimed to quantify and compare seedling recruitment and population expansion in both study species following disturbance. Results were related to the regenerative modes of both species.

1.2.4 PRACTICAL SIGNIFICANCE

This study is not only of academic value but is important for fynbos management. Current conservation management policies aimed at the maintenance of species diversity are influenced by previous research findings. Thus, it is imperative that those families which have hitherto been neglected receive more attention. An understanding of the basic biology of the principle thatching reed species, as well as the dynamics of disturbed populations, will assist in the understanding of restioid fynbos. The implications of removing large amounts of seed by harvesting of the study species on the seed bank dynamics are discussed. Attempts are made to predict the effects of different harvesting regimes used in the commercial exploitation (i.e. inter-harvesting periods, harvesting height and season) on seed bank dynamics of both study species. This information was used to develop ecologically based management guidelines, using both prescribed brushcutting and burning as management tools, for the sustainable utilization of the two thatching reed species.

1.3 STUDY AREA AND STUDY SITES

1.3.1 PHYSIOGRAPHY, CLIMATE, VEGETATION OF THE AGULHAS PLAIN

The bulk of the study was carried out at two study sites, situated on the Agulhas Plain in the south-western Cape, South Africa (Figure 1.1). The Agulhas Plain is an area occupying approximately 1500 km^2 of rolling landscape at the southern tip of the African continent. The mediterranean-type climate of the area is fairly uniform, with cool winters and warm summers. The majority of the rain falls in winter, although there is occasionally summer rain which alleviates moisture stress (Miller *et al.* 1983, Specht and Moll 1983, Stock *et al.* 1992). The area falls within the Cape Floristic Region (Bond and Goldblatt 1984) and is dominated by fynbos vegetation types, an evergreen, sclerophyllous, heath-like shrubland

associated with nutrient poor soils (Cowling *et al.* 1988). The vegetation bears similarities to other fire-prone shrublands of Mediterranean-climate regions, especially the kwongan of south western Australia (Cowling and Witkowski 1994). The coastal forelands of the fynbos biome are characterized by high floristic and vegetational complexity (Boucher 1987). The Agulhas plain is an exceptionally species-endemic rich lowlands area (Cowling 1990, Cowling and Holmes 1992, Cowling *et al.* 1992, Willis *et al.* 1995). The lack of conservation planning, together with increasing levels of cultivation, overgrazing, brushcutting, infestation of alien plants and general poor management in the region is resulting in the rapid deterioration of natural vegetation (Taylor 1978, Boucher and Moll 1980, Jarman 1986, Rebelo and Siegfried 1990).

1.3.2 STUDY SITES

The two study sites (Plate 1.1), Zoetendalsvallei (*T. insignis*) (34^0 44' 57"; 20^0 00' 9") and Zeekoeivlei (*T. erectus*) (34^0 39' 38"; 20^0 02' 35") are 10 km apart and 5 km and 8.75 km from the coast, respectively (Plate 1.1). The field work for the study on the effects of disturbance on vegetative regrowth was undertaken at De Hoop Nature Reserve, 64 km NE of Cape Agulhas (Plate 1.15). A description of the two sites at De Hoop Nature Reserve is found in Chapter 3. Physiographic, climatic and floristic data for both study sites are summarized in Table 1.1.

It should be noted that the experimental design involved subsampling a given population rather than true replication provided by sampling a number of matched populations. It would have been desirable to have sampled replicate populations of each study species, but given the logistic constraints (including limited laboratory and greenhouse space) this was not possible. The study sites and populations chosen, however, were considered representative of the study species.

Each study site comprised of a gently sloping (< 10°) homogeneous area of approximately 200 m X 200 m, situated in a much larger area of similar vegetation. Both study species were dominants and had consistently high cover over the respective study sites. After the 1992 reproductive season, a 100 X 200 m block comprising approximately half of the study site was harvested. Five plots of 10 m X 10 m were randomly located in both the unharvested (control) and harvested vegetation (Plate 1.2). Plot boundaries were marked and an identification tag was placed on a corner marker. Plots were located at least 30 m away from boundaries between harvested and unharvested vegetation to minimize "edge effects". Both study species were harvested after seed dispersal and before the following year's cohort of new culms had reached a height at which brushcutting would damage the growing culm tips (hereafter referred to as the critical height). Both populations of the study species had culms of marketable length. Techniques normally used to harvest thatch in the area (as explained in section 1.4) were used.

At both sites, the fairly shallow soils were unconsolidated, structureless colluvial sands (Fernwood form) of mixed origin (calcareous sands or Table Mountain Group sandstone) which were well-drained (Thwaites and Cowling 1988). Excavations revealed that the soils overlie Bredasdorp formation limestone (0.25-> 0.9 m) at the *T. insignis* site and a hard orange-brown Table Mountain Group sandstone (0.20-> 0.5 m) at the *T. erectus* site. Soils at the *T. erectus* site are older, better developed, finer and browner in colour than those at the *T. insignis* site (Thwaites and Cowling 1988). The soils at the *T. insignis* and *T. erectus* sites are slightly acidic (pH 5.59 ± 0.26 and 5.12 ± 0.68, respectively (n = 5) (Scofield and Taylor 1955)).

Zoetendalsvallei and Zeekoeivlei are 9.25 km and 19 km north of Cape Agulhas (the closest weather station), respectively. Climatic data from this weather station have been used in this study. The climate is mild and frost free, with a mean annual temperature of 17.2°C (calculated for the period 1961-1990; Department of Environment Affairs, unpublished data). Mean

annual rainfall measured at Cape Agulhas is approximately 460 mm (calculated for the period 1894-1993; Department of Environment Affairs, unpublished data). Historically, approximately 65% of annual precipitation falls in the winter months (May-October). During the year preceeding and during the data collection period of this study (i.e. 1991-1993), annual rainfall was higher than the mean annual rainfall for two years (1992 = 527.5 mm; 1993 = 631 mm) and lower than the mean annual rainfall for one year (1991 = 408.9 mm). During the same period, mean monthly temperatures ranged from 24°C in January to 15.9°C in July. The area is extremely windy with mean daily winds, usually easterly in direction, exceeding 300 km day^{-1} during the summer months (Deacon *et al.* 1992). As a result, the study sites are wind swept and dry in summer. Climatic data are displayed in Figure 1.2.

Using the same method as Cowling *et al.* (1988), the fynbos vegetation at the Zoetendalsvallei and Zeekoeivlei study sites was classified as Dry Restioid Fynbos. This vegetation type is tall, dense restioveld (> 60% restioid cover) with a sparse shrub stratum (< 30 %) (Campbell *et al.* 1981). Both study sites were free of alien vegetation.

As is typical of fynbos, communities at both study sites are fire-prone and subject to recurrent fires at a 10 to 30 year interval, although extremes of 4-40-year cycles are possible (Bond 1984, Kruger and Bigalke 1984, Cowling *et al.* 1987b). Fires are most likely to occur during the dry, windy summer months, although, large fires can also occur in winter under bergwind conditions (van Wilgen 1984).

The *T. insignis* study site was most recently burnt in 1981 (M. van Breda *pers. comm.*). The thatch had not been harvested since the last fire (i.e. 11 years of growth had taken place). The vegetation appeared to be fairly even-aged (as indicted by the remarkably uniform tussock diameter and plant height), as is expected when recruitment is limited almost exclusively to the immediate post-fire years (Kruger 1984). Total projected foliage cover was

approximately 80%. The community was dominated by *T. insignis* (53% projected foliage cover) and *Metalasia brevifolia* (10%). Other common ericoid shrubs included *Passerina vulgaris* (5%), *Aspalathus* spp. (5%), *Nylantia spinosa* (3.8%), *Phylica ericoides* (3%), *Agathosma* spp. (< 1%) and *Erica* spp. (< 1%). *Rhus glauca* (2%), and *Euclea racemosa* (1%) were the common large-leaved (non-proteoid) shrubs. Other graminoids, forbs, geophytes, creepers, succulents and annuals were rare (< 1%). Proteoids were rare (< 1%). The study site has moderate to low species richness (38 species in total). *Thamnochortus insignis* plants were vigorous; with the majority of culms being green.

The vegetation community at Zeekoeivlei ranges from open to dense shrubland and was mature, being at least fifteen years since the last fire. Total foliage projected cover was approximately 80%. The community was dominated by *Thamnochortus erectus* (40% projected foliage cover) and *Sideroxylon inerme* (35%). *Rhus glauca* (2%), *Pterocelastrus tricuspidatus* (< 1%), *Carissa bispinosa* (< 1%) and *Euclea racemosa* (< 1%) were other common large-leaved (non-proteoid) shrubs. The prolonged absence of fire in this community and high soil nutrients, has resulted in the establishment of resprouting, wind and bird dispersed subtropical thicket precursors (Knight 1988) and the development of patches of a closed thicket community, which is generally not fire prone (Taylor 1961, Cowling 1984, Tinley 1985, Cowling and Pierce 1988, Manders 1990). Members of Poaceae, namely *Pentaschistis* spp. (11%), *Sporobolus africanus* (3%), *Cynodon dactylon* (2%) and *Eustacys mutica* (< 1%) were also common and formed a dense field layer in places. Ericoid shrubs, other graminoids, forbs, geophytes, creepers, succulents and annuals were rare. Proteoids were absent. The study site has a moderate to low species richness (35 species in total). *Thamnochortus erectus* plants were fairly vigorous, although some plants were senescent towards the centre of the tussock.

1.4 STUDY SPECIES AND THATCHING INDUSTRY

The Restionaceae (Monocotyledoneae) are almost exclusively found in the southern hemisphere (Linder 1985), which has resulted in the family being regarded as a Gondwanan relic (Linder 1987). The mediterranean type ecosystems of south western South Africa (*ca.* 300 species) and south western Australia (*ca.* 100 species) support the vast majority of the 430 species in this family (Linder 1985). Species of Restionaceae are more prominent and widespread in fynbos than in kwongan communities (Levyns 1961, Milewski and Cowling 1985). In both regions, the plants occur mainly on nutrient-poor soils (Specht 1981). As well as being one of the three families defining fynbos, Restionaceae is one of the 10 largest families in the vegetation type and approximately 300 species are endemic to the Cape Floristic Region (Taylor 1978, Bond and Goldblatt 1984). The Agulhas Plain supports 98 species (Cowling and Holmes 1992). There are approximately 31 species belonging to the genus, *Thamnochortus*, in the Cape Floristic Region (Bond and Goldblatt 1984). Shallow, intensive rooting systems serve to capture most of the water that enters the soil profile and enables plants to survive in very dry or seasonally waterlogged habitats (Stock *et al.* 1992). Despite being ecologically important in the Cape Floristic Region (Linder 1991), Restionaceae have not been as intensively studied as have their counterparts in Australia, especially in respect to their reproductive biology, life history traits and fire regenerative modes (e.g. Meney and Dixon 1988, Meney *et al.* 1990a, 1990b; Pate *et al.* 1991, Brown *et al.* 1994, Meney *et al.* 1994).

Thamnochortus insignis and *Thamnochortus erectus* (Plate 1.3 and 1.4) are dioecious perennials and form a conspicuous above-ground component of the fynbos communities in which they are found. Both *T. insignis* and *T. erectus* grow as tall tussocks of unbranched culms, 0.35-2.5 and 0.33-1.5 m high, respectively (Plate 1.5). These culms arise from a simple and interwoven rhizomatous subterranean base. *Thamnochortus erectus* forms a roughly circular tussock, with new culms on the periphery and older

senescent culms towards the center. This gives the plant an untidy appearance, which is in contrast to the elegant tussocks of *T. insignis*. Both species have simple fertile scapes and subglobose female spiklets (Plate 1.3 and 1.4). The species differ in that *T. insignis* has spiklets ranging from 15 to 25 mm and *T. erectus* has spiklets up to 10 mm in length. The two closely related study species seldom co-occur. *Thamnochortus insignis* is common on grey, slightly acidic sands at the base of the limestone dunes or sandy flats of coastal forelands and has a natural distribution range from Gouritz River mouth near Albertinia to a short distance west of Bredasdorp in the Caledon region (Linder 1985) (Figure 1.1). Commercial exploitation has resulted in its introduction in disturbed areas along the coast from Hermanus to Cape St Francis. *Thamnochortus erectus* is common on older brown-grey dune sands and flats of coastal forelands and has a natural distribution range from Darling (near Malmesbury) to Knysna (Linder 1985) (Figure 1.1). It is estimated that *T. insignis* plants have a life-span of approximately twenty years (Linder 1990) and *T. erectus* plants are longer-lived with an estimated lifespan of 80-100 years. Characteristics of *T. insignis and T. erectus* are summarized in Table 1.2.

In the past, many species of Poaceae and Restionaceae were used to construct shelters, and later, as a roofing material for houses in the south-western Cape (Clegg 1980, Linder 1990). Over the years the demand for thatch has fluctuated as fashions changed and other roofing materials became available. *Thamnochortus insignis* (Albertinia dekriet or mannetjiesriet) and to a much lesser extent *T. erectus* (wyfieriet) have been exploited commercially from natural or near-natural stands periodically. Owing to the unregulated nature of the industry the present size of market is difficult to estimate. Alien vegetation is kept low in thatch stands, and thus management of large areas of fynbos for thatch production may contribute to the conservation of Restioid Fynbos. The industry provides a valuable source of income to small-scale farmers and local self-employed thatch cutters and roof-thatchers. An approximately 10 cm diameter *T. insignis* and *T. erectus* thatch bundle is sold by the farmers for R0.65 and

R0.55, respectively (1994 values). Thatch cutters receive approximately 5% of this value (1994 value). The annual crop has been estimated to be worth R5-10 million (Linder 1990). In recent years, thatch-roofed houses have become sought after in wealthier suburbs, holiday resorts and in eco-sensitive developments (Plate 1.6). The increased demand for thatch has resulted in an interest in its cultivation among farmers (Linder 1990). There, thus, appears to be a high potential for increased harvesting of this resource and consequently danger of mismanagement.

Populations of *T. insignis* are usually harvested seven to ten years after fire, and approximately every five years subsequently (in many cases more frequently). Harvesting occurs from late autumn to mid-winter (May-August) after the seed has set. Many farmers, however, allow teams of thatch cutters to harvest outside this period when other farming activities deliver poor returns (M. van Breda *pers. comm.*). This often results in harvesting of thatch before seed maturation and dispersal, and increased harvesting frequencies. Harvesting is non-selective and all of the culms are removed from the tussock at a height of approximately 50-70 mm by a mechanized brushcutter (Plate 1.7). Plants that escape harvesting are either very small individuals (diameter < 50 mm) or individuals or parts of individuals that are inaccessible, growing between fynbos shrubs. The next cohort of culms begins to grow in winter (June to July), shortly after harvesting and emerges above the cropped stubble in early spring (August to September) (Plate 1.8). The culms continue to grow and by early summer (October) bear immature inflorescences. Wind pollination occurs in late summer (February). The seeds are light golden-tan in colour and become darker brown in colour with burial in the soil. The seeds have a persistent perianth which acts as a wing (Plate 1.3) and wind-borne dispersal occurs from the end of autumn (mid-April) to mid-winter (July) once the seed is mature. The first seedlings germinate in late winter (July-August). For the first few years the seedlings bear small, sterile, curly branched culms with relatively well-developed leaves, which are thought to accumulate resources for the new plant (Plate 1.9). After a few years the first straight, unbranched fertile culms with

brown sheaths appear and eventually the tussock comprises of only this culm type. After harvesting, culms are either left to dry on the ground for 4-6 weeks or immediately gathered up, bundled and stacked in conical shaped ricks to dry (Plate 1.10). Old or short culms are discarded and form a layer of litter partly or totally covering the bare harvested patches. In many areas the natural veld is managed in such a way as to promote the expansion of the thatch tussock and increase thatch yields per unit area. The co-occuring fynbos shrubs are removed by brushcutting and this has possible short- and long-term implications to the conservation status of natural areas managed in this way (Ball 1991).

Populations of *T. erectus* are harvested for use in the thatching industry or by farmers to combat erosion in blow-outs, wash-aways etc. (P.K. Albertyn *pers. comm.*) (Plate 1.11). *Thamnochortus erectus* thatch is of inferior quality compared to *T. insignis*, and is therefore usually only harvested in times of great demand. Culms tend to be shorter and thinner and there is a higher percentage of dead culms in the tussock (pers. obs.) (Plate 1.5). Plants are harvested in the same way as for *T. insignis* and the pattern of harvesting also follows the developmental cycle of the plant. Populations of *T. erectus* are harvested from summer to autumn (December to April), after seed set. The next cohort of culms begins to grow in mid-autumn (April), shortly after harvesting and emerges above the cropped stubble in late autumn (May). The culms continue to grow and by mid-winter (July) bear immature inflorescences. Wind pollination occurs from late winter to spring (August to September). The seeds are light brown in colour and become a darker brown with burial in the soil. The seeds have a persistent perianth which acts as a wing (Plate 1.4) and wind-borne dispersal occurs in summer (November to March) as soon as the seeds are mature. The first seedlings germinate from mid-autumn to mid-winter (April to June) in the field.

1.5 METHODOLOGY

Many different methods on different levels of organization, namely individual and population, were used in this study. This involved removing the current years seed crop from in and around the plots by harvesting and comparing the seed bank dynamics in these plots to that in controls. Seed bank dynamics were studied in a number of ways. Before this study was initiated the literature on seed bank methodology was critically reviewed. The methods used in the study were chosen after careful consideration of the research questions and goals needing to be addressed. An experimental approach was used, an approach seldom used in seed bank studies owing to the tedious nature of the work and logistic constraints. Both inputs and losses to the seed bank were studied for two consecutive years. Seed production was monitored by bagging culms. Pre- and post-dispersal predation losses were determined. Estimates of seed bank sizes were made at intervals using two methods, namely a physical separation technique utilizing sieving and direct seed counts and a seedling emergence technique. This provided a more precise estimate of seed bank size than either technique alone (Conn *et al.* 1984). Suggestions for methodology for similar studies in lowland fynbos were based on comparisons of the two methods. Problems with many seed banks studies have included the failure to sample throughout the year and in more than one year, insufficient number of samples, lack of controls, and failure to analyze the data statistically (Simpson *et al.* 1989). This study attempted to avoid these problems. The estimates of seed bank size were used together with seed decay experiments, to asses the persistence of seed banks. Seed decay was monitored at intervals over an eighteen month period using two different methods. Mesh burial bags and boxes were used to determine seed decay, germination and survival with time. The design of the mesh boxes ensured that conditions inside the box were more similar to those of the surrounding environment, than inside the mesh bags. Differences in results obtained using the boxes were compared to those obtained using bags, the technique most commonly used in decay experiments. A separate field study compared plant mortality,

vegetative regrowth and seedling recruitment in mature undisturbed fynbos with that of disturbed areas (i.e. burnt and harvested). The germination requirements of the two study species were not studied in detail. A "seed budget" (Mallik *et al.* 1984, Andersen 1989) was constructed using estimates of seed production, seed bank size, pre- and post-dispersal seed losses to predation, and losses of soil-stored seeds to predation, decay and germination. An estimate of the seed budgets of both species was also constructed using data from harvested areas. It was, thus, possible to place the seed bank studies in context, relative to other life history phases, and to asses the limits to population recruitment after disturbance.

Statistical analyses included parametric techniques and log-linear analyses. The statistical package Statgraphics 6.0 (STSC Inc.) was used to analyze most of the data. The seed bank study consisted of count data with many zero values. Generalised linear models (statistical package: GLIM, Baker and Nelder 1978) was used to analyze the seed bank data (McCullagh and Nelder 1983). This technique avoids the assumptions of normality associated with many statistical procedures (Zar 1984, Crawley 1993). The technique is extremely powerful and broad-ranging. It also fosters a more critical approach to statistical analyses. Despite these strengths and the fact that the package has been available for a period of time, very few studies have used it to analyze seed bank data. This is possibly due to the "user unfriendly" nature of the package.

1.6 THESIS STRUCTURE AND OUTLINE

The thesis consists of four chapters, including this introductory chapter which provides a general introduction to the study. The chapters following will form the main body of the thesis, where the main findings will be presented and discussed. They are written in a format that can easily be reduced for scientific publication. This has meant that some details have been repeated in more than one chapter. These chapters are also longer than would be required for publication, primarily due to the more extensive

literature review and discussion required for a thesis. Chapter 2, deals with pattern and process at population level and comprises an investigation into the seed bank dynamics and field seedling establishment (Plate 1.12, 1.13 and 1.14). Chapter 3 is a study on the effect of fire and harvesting on the population dynamics of the two study species (Plate 1.8 and 1.16). The concluding chapter will highlight the major findings of the study, as well as the limitations. The appendices comprise studies of a limited nature that are related to the main study. This thesis is designed to be able to be read in different parts and in different sequences depending on the level of detail required by the reader.

Plate 1.1. The Agulhas Plain study sites: *(Top)* Zoetendalsvallei (*T. insignis*) and *(Bottom)* Zeekoeivlei (*T. erectus*).

Plate 1.2. Zoetendalsvallei (*T. insignis*) study site after approximately half the area was harvested.

Plate 1.3. *Thamnochortus insignis* Mast.

(A) Female culms with mature inflorescences (note: culms are stout; inflorescences exceed 10 cm and are branched); (B) female culms with immature inflorescences; (C) male culms with mature inflorescences; (D) male culms with immature inflorescences; (E) whole plant; (F) female flower (note: perianth often obscured by bracts) and (G) male flower (Artist - Ellaphie Ward-Hilhorst).

THAMNOCHORTUS INSIGNIS F.3 X8

THAMNOCHORTUS INSIGNIS.

Plate 1.4. *Thamnochortus erectus* (Thunb.) Mast.

(a) Female culms with mature inflorescences (note: culms are stout; inflorescences exceed 10 cm and are branched; spiklets ovate, obovate or rotundate, light brown); (b) female culms with immature inflorescences; (c) male culms with immature inflorescences; (d) male culms with mature inflorescences; (e) whole plant; (f) female flower (note: perianth protruding from sides of bracts) and (g) male flower (Artist - Vicky Thomas).

f.g. × 8 Thamnochortus erectus L. Thomas

ERECTUS

Plate 1.5. Whole-plant aspects of: *(Top) T. insignis* and *(Bottom) T. erectus.*

Plate 1.6. Harvested *T. insignis* being used as thatching material in: *(Top)* a rural community and *(Bottom)* an eco-sensitive development.

Plate 1.7. Harvested individuals (note: height of harvesting above the ground, thatch lying on the ground before collection).

Plate 1.8. New culm growth in *T. insignis*: *(Top)* four months and *(Bottom)* twelve months after harvesting.

Plate 1.9. *Thamnochortus insignis* seedlings (note: branched and unbranched unreproductive culms).

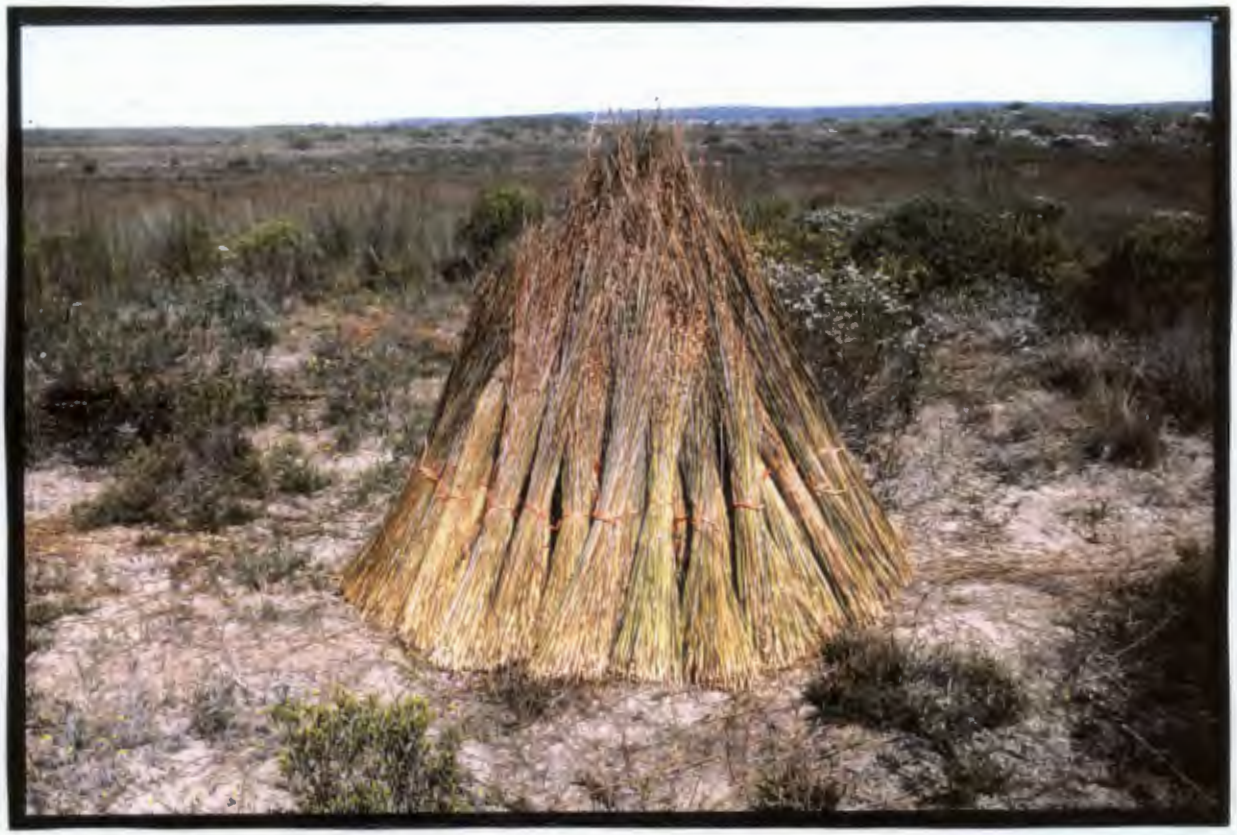


Plate 1.10. Harvested thatch stacked in conical-shaped ricks in the thatching reed veld.

Plate 1.11. Harvested *T. erectus* being used to combat erosion.

Plate 1.12. Instrument used for soil coring and "holes" remaining after soil cores have been taken for the seed bank study.

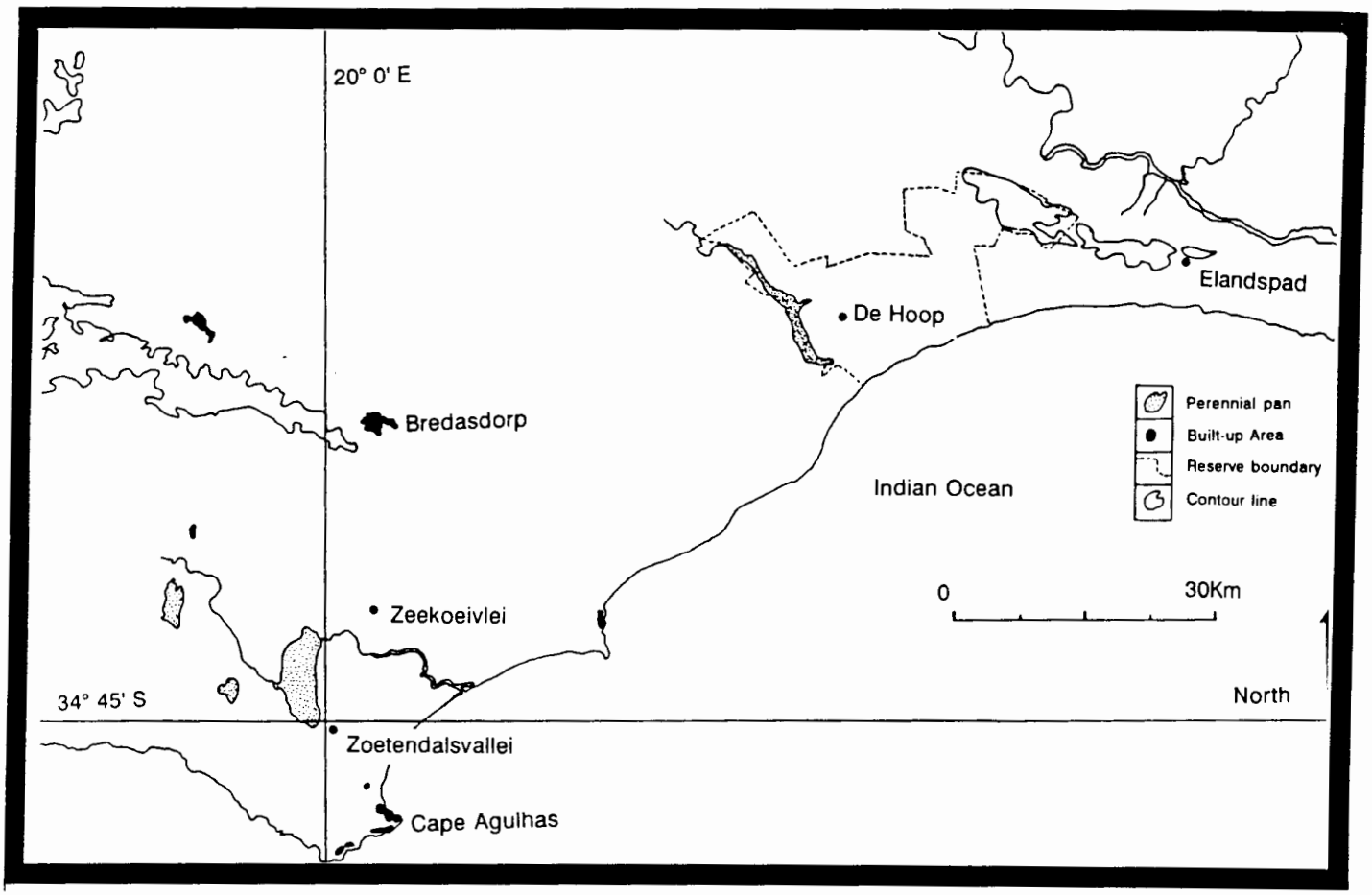
Plate 1.13. Burial bags used in the seed decay experiment: *(Top)* before burial and *(Bottom)* after excavation 16 months later (*T. erectus*).

Plate 1.14. Burial boxes used in the seed decay experiment: *(Top)* buried in the field and *(Bottom)* opened during excavation 16 months later (note: branched seedlings).

Plate 1.15. De Hoop Nature Reserve study sites: *(Top)* De Hoop farm (*T. insignis*) and *(Bottom)* Elandspad (*T. erectus*).

Plate 1.16. Vegetative regrowth of the study species after fire: *(Top) T. insignis* (note: seedling with branched and unbranched unreproductive culms) and *(Bottom) T. erectus*.

Figure 1.1. Map indicating the location of the study sites, Zoetendalsvallei and Zeekoeivlei, Bredasdorp.



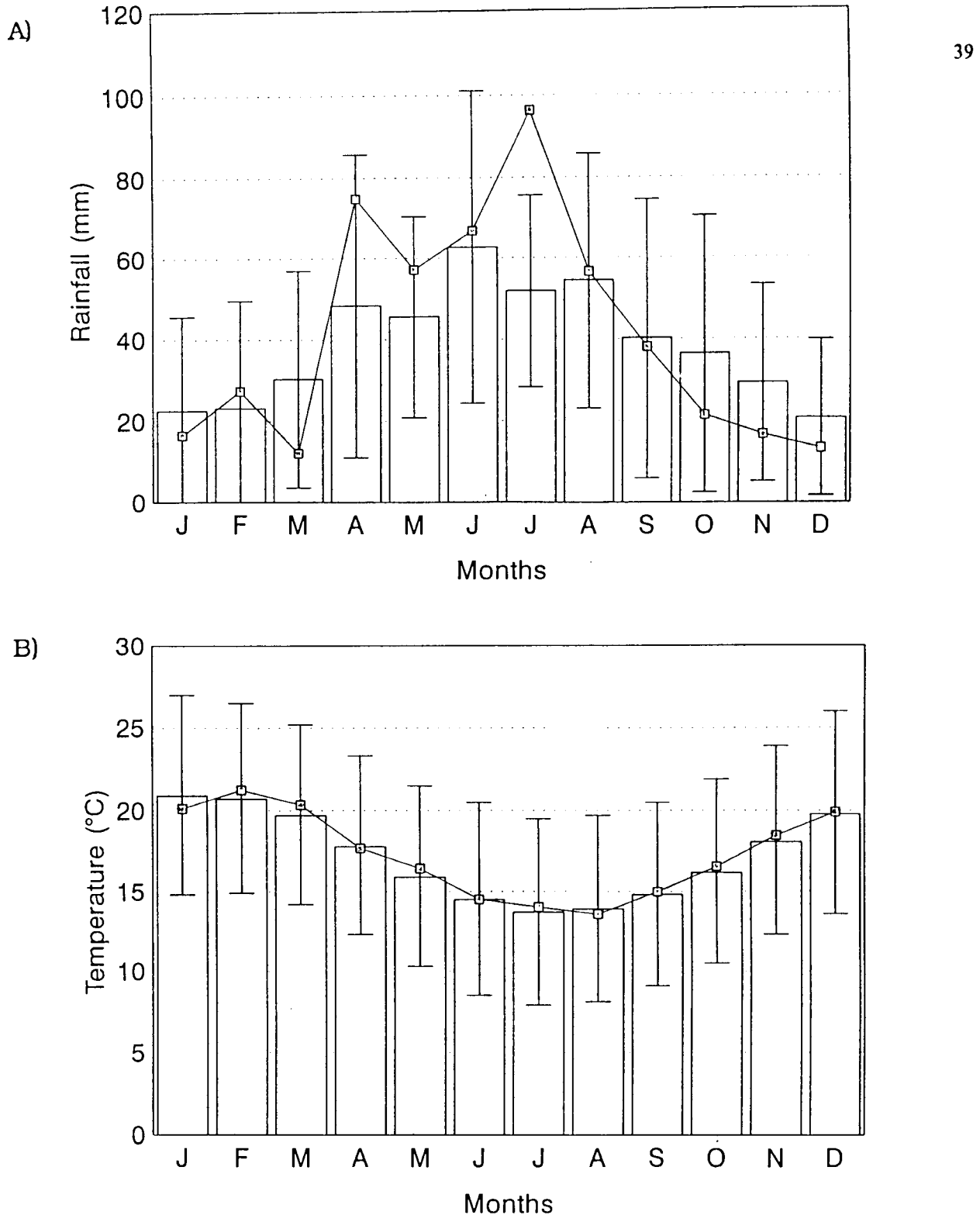


Figure 1.2. Climate diagram for the study sites, Zoetendalsvallei and Zeekoeivlei. Data are from the Cape Agulhas meteorological station (Weather Bureau).

A) Mean monthly rainfall (1894 to 1990) and for study period (from 1990 to 1993) at Cape Agulhas. S.D. are displayed.

B) Mean monthly temperature in degrees Celsius (°C) (from 1961 to 1990) and for the study period (from 1990 to 1993) at Cape Agulhas.
S.D. are displayed.

Table 1.1. Physiography, climate and flora of the study sites, Zoetendalsvallei and Zeekoeivlei, Bredasdorp.

	Study site	
	T. insignis	T. erectus
Physiography		
Soils [a]	Unconsolidated, structure-less colluvial sands of mixed origin	Unconsolidated, structure-less colluvial sands of mixed origin
Depth	0.25 - > 0.9 m	0.20 - > 0.9 m
Age	Recent	Older
Texture	Fine - medium	Fine
Colour	Grey	Grey - brown
pH [b]	5.59 + 0.26	5.12 + 0.68
Bedrock	Bredasdorp limestone	Table Mountain sandstone
Climate		
General	Mediterranean type Mild, frost-free	Mediterranean type Mild, frost-free
Mean annual rainfall [c]	460 mm 65 % in winter (May - Oct)	460 mm 65 % in winter (May - Oct)
Mean annual temperature [d]	17.2 C	17.2°C
Mean monthly temperature - Maximum [e]	24°C (January)	24°C (January)
- Minimum [e]	15°C (July)	15°C (July)
Wind speed (mean daily winds) [f]	Windy; 300 km per day	Windy; 300 km per day
Wind direction [f]	Easterly	Easterly
Flora [g]		
Fynbos type	Dry restiod fynbos	Dry restiod fynbos with thicket patches
Years since last fire	11 years [h]	> 15 years [i]
Total projected foliage cover	Ca. 80 %	Ca. 80 %
Dominants (% projected foliage cover)	T. insignis (53 %)	T. erectus (40 %)
Life forms		
Ericoid shrubs	Common (28 %)	Rare (< 1 %)
Proteoid shrubs	Rare (< 1 %)	Absent (0 %)
Large-leaved (non-proteoid) shrubs	Common (3 %)	Very common (39 %)
Grasses	Rare (< 1 %)	Common (17 %)
Graminoids (other than study species)	Rare (< 1 %)	Rare (< 1 %)
Forbs	Rare (< 1 %)	Rare (< 1 %)
Geophytes	Rare (< 1 %)	Rare (< 1 %)
Succulents	Rare (< 1 %)	Rare (< 1 %)
Annuals	Rare (< 1 %)	Rare (< 1 %)
Alien species	Absent (0 %)	Absent (0 %)
Species richness	Moderate-low (38 species)	Moderate-low (35 species)

[a] Thwaites and Cowling 1988.

[b] This study - Mean ± standard deviation (n = 5).

[c] Department of Environmental Affairs, unpublished data (1894-1993).

[d] Department of Environmental Affairs, unpublished data (1961-1993).

[e] Department of Environmental Affairs, unpublished data (1992-1993).

[f] Deacon *et al.* 1992.

[g] This study, using the same methods as Cowling *et al.* 1988.

[h] M. van Breda, personal communication.

[i] P.K. Albertyn, personal communication.

Table 1.2. Characteristics of the study species, *Thamnochortus insignis* Mast. and *Thamnochortus erectus* (Thunb.) Mast. , Restionaceae.

[a] Bond and Goldblatt 1984.

[b] This study.

Characteristic	Species	
	T. insignis	T. erectus
Distribution	Gouritz River mouth to west of Cape Agulhas	From Darling (near Malmesbury) to Knysna
Habitat	Coastal forelands, on young poorly developed sands (0.25-<1m) derived from Bredasdorp Formation limestone	Coastal forelands, on older, better developed sands
Plant height (m)	< 2.5 m	< 1.5 m
Pollination syndrome	Wind	Wind
Dispersal syndrome	Wind	Wind
Flowering	October to March (summer)	August to November (spring)
Pollination	February (summer)	August to September (spring)
Seed dispersal	April to July (autumn to winter)	August to September (winter to spring)
Seed germination	July to August (winter)	April to June (autumn to winter)
Vegetative growth	June to September (winter to spring)	April to May (autumn)
Harvesting	May to August (winter)	December to April (summer to autumn)
Post-fire response	Non-sprouter	Sprouter

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CHAPTER 2

SOIL-STORED SEED BANKS OF TWO THATCHING REED SPECIES: PERSISTENCE AND DYNAMICS IN RESPONSE TO HARVESTING

2.1 ABSTRACT

Seed characteristics, population structure, pre- and post-dispersal seed losses, seed production, soil seed bank dynamics and seedling establishment of two thatching reed species, namely *Thamnochortus insignis* Masters and *Thamnochortus erectus* (Thunb.) Masters (Restionaceae), were investigated on the Agulhas Plain. The study species are both perennial hemicryptophytes each with a different regeneration mode, the former being a non-sprouter and the latter a resprouter. The effects of harvesting on all aspects of the soil seed banks were determined.

Both pre- and post-dispersal soil cores were collected to determine seasonal variation in seed banks. Seed persistence in both burial boxes and bags were recorded at intervals over 16 months. A "seed budget" was used to integrate the important processes influencing seed bank density, and to investigate similarities and differences between the study species. Both species produced considerably more plump seeds than were incorporated into the seed bank (approximately 3.5 times) and it was during this life history stage that the largest seed losses (approximately 80% of annual seed production) were observed for both species. Seed bank densities of both species were high; with that of *T. insignis* being approximately 1.5 times larger than that of *T. erectus*. This was attributed to greater seed production, rather than to longer survival of seed in the soil. The seed bank densities of both species were distinctly seasonal, with substantially larger seed banks being recorded shortly after seed production and dispersal (*T. insignis*: 31 times; *T. erectus*: 2.2 times). Using the physical separation technique, *T. insignis* average annual seed bank size varied between 1633 ± 2601 seeds per m^2 before dispersal, and 3773 ± 6027 seeds per m^2 after dispersal, while those of *T. erectus* varied between 1134 ± 2644 seeds per m^2 before dispersal and 2530 ± 3482 seeds per m^2 after dispersal. Seed bank estimates from germination were approximately 3.5 times lower than those from direct seed counts. Annual seed production and seed bank densities of both species showed large annual variations, as well as variation between

species. An accumulation of seeds in the soil over the two years was observed for both species. Harvesting resulted in a drastic decline in both seed production (*T. insignis*: 99%; *T. erectus*: 99%) and post-dispersal seed bank density (*T. insignis*: 45%; *T. erectus*: 85%) for both species. Harvesting action resulted in active dispersal of seed, and consequently an increase in pre-dispersal seed bank density for both species. Both species had seasonally persistent seed banks, and seed losses over the year following seed input were moderate (*T. insignis*: 12% of annual seed input; *T. erectus* 25% of annual seed input). Seed burial showed that seed persistence and losses in seed banks differed between species and experimental seed bank type. *Thamnochortus erectus* showed greater seed persistence (1.20 times) and *T. insignis* showed greater seed losses (3.25 times) after 16 months burial. These results conflicted with actual observations of seed bank densities. Burial boxes showed greater seed persistence (*T. insignis*: 1.43 times; *T. erectus*: 1.1 times) and burial bags showed greater seed losses (*T. insignis*: 2.10 times; *T. erectus*: 3.02 times) for both species after 16 months burial. Inter-fire recruitment of both species was limited in mature vegetation, although that of *T. insignis* was approximately 11 times greater and more variable than for *T. erectus*. The "open" microhabitat was favoured by seedlings of both species. Seedling survival, especially for *T. insignis* was low, with few seedlings being greater than one year of age.

The study provided comparative insights into the biology of the two allopatric and closely related species. The results are discussed in relation to other life-history attributes and regeneration modes of the species. Implications of results for commercial harvesting of the species are also discussed.

Key words: Direct seed count, dispersal, harvest, seasonal persistence, soil-stored seed bank, seedling recruitment.

2.2 INTRODUCTION

Seed bank studies are an important consideration in the development of a predictive understanding of plant population structure and function (Roberts 1981, Leck *et al.* 1989). In fire-prone shrublands, where the seed and seedling stages are critical stages in the life cycles of most plants, seed banks play a major role in population dynamics. For many species, the replacement of populations after a disturbance is determined primarily by the availability of either soil-stored or canopy-stored (serotiny) seed (Naveh 1974, Gill 1981a, 1981b).

Canopy-stored seed banks have been extensively studied in mediterranean-type ecosystems, including fynbos (e.g. Bond *et al.* 1984, Van Wilgen and Viviers 1985, Bond 1985, Cowling *et al.* 1987a, Midgley 1989, Lamont *et al.* 1991, Pannell and Myerscough 1993, Bond *et al.* 1995).

Soil-stored seed banks have been fairly well studied in many diverse habitats, including fire-prone shrublands (Leck *et al.* 1989). Fire-prone shrublands in which studies have been conducted, include Californian chaparral (e.g. Keeley 1977, 1987, Kelly 1986, Zammit and Zedler 1988, 1994), Australian shrublands (e.g. Auld 1986a, Meney *et al.* 1994) and European *Calluna* heath (e.g. Mallik *et al.* 1984, Willems 1988). These studies indicate that soil seed banks in these vegetation types are often large and persistent (i.e. seed survives for more than one year) which enables the replacement of species after fire (Thompson and Grime 1979). There is also evidence for large variations in the sizes of soil seed banks for different species at different sites (Leck *et al.* 1989).

Despite the large number of seed bank studies undertaken in fire-prone shrublands there are still several unanswered questions. Little is known about the size and dynamics of entire seed banks within these vegetation types, as most studies have focused on individual dominant species. Furthermore, most studies have focused on the reproductive differences

among woody resprouters and non-sprouters (e.g. Lamont 1985, Cowling and Lamont 1987, Cowling *et al.* 1987a). Spatial and temporal dynamics of seed banks have been poorly documented (Van der Valk and Pederson 1989). Data on seed longevity are scarce and mostly from laboratory studies, which does not allow for the incorporation of environmental conditions experienced by buried seeds. Little is known about seed predation rates and whether predation rates are reflected by differences in seed dormancy. There also appears to be a general lack of consistency in results obtained from many of the studies (Parker and Kelly 1989).

Research on soil seed banks in fynbos has centered on the seed and seedling ecology of shrubs of the Proteaceae, Ericaceae, Rhamnaceae, Thymelaeaceae, Rutaceae, Asteraceae and Polygalaceae (e.g. Le Maitre 1988, Pierce and Cowling 1991a, 1991b; Manders 1990b, Musil 1991, Kilian and Cowling 1992). Thus, although, soil-stored seed banks in fynbos shrubs have been reasonably well studied there are major gaps in our knowledge with respect to the seed biology and, more specifically, the seed bank ecology of the non-shrub component of the vegetation type. Fynbos communities are often dominated by herbaceous, rush-like perennials belonging to the family Restionaceae. Despite being a family that is economically important, and physiognomically and floristically characteristic of the fynbos, the only research carried out thus far on South African members of this family has been by Musil (1991) on *Thamnochortus punctatus* (Milewski and Esterhuysen 1977, Linder 1985, 1991).

A knowledge of the dynamics of seed banks of component species is important for predicting their persistence in a community (Parker *et al.* 1989). Seed bank dynamics are affected by rates of seed input by parent plants and immigration, redistribution of seed, and losses due to decay, predation, death, deep burial, germination and emigration (Simpson *et al.* 1989). The longevity of seeds in the soil is the most important dynamic characteristic of seed banks.

Persistent seed banks are selected where species depend on seeds to maintain the population through a period of risk (Parker *et al.* 1989). As a method of regeneration, persistent seed banks are fundamental to the maintenance and expansion of populations of a large number of species in fire-prone shrublands (Bond *et al.* 1984), and this distinguishes them from other communities (Parker and Kelly 1989).

Non-sprouting species in fire-prone shrublands face the risk of the death of the parent plant before or at the time of fire, with future survival depending on seed banks (Keeley 1991). When recruitment is limited to the post-fire period, the long-term persistence of seeds may ensure population survival from the time of parent plant death until the next fire (e.g. Keeley and Zedler 1978, Keeley and Keeley 1989, Parker and Kelly 1989). Seasonal persistence of seeds for more than one year will also ensure population replacement in any season, after fire. Thus, even if adult plants survive the full fire cycle, seasonal persistence of seeds may be advantageous. Persistent seed banks can also protect populations from local extinction, caused by reproductive failure in a poor year, in variable environments (Cohen 1966) and can allow seed banks to attain a large size that is not possible with a single year's seed production (Cavers 1983).

Not all species in fire-prone environments have persistent seed banks. In chaparral and fynbos, many species have transient seed banks, where seed either germinates or deteriorates shortly after dispersal and incorporation into the seed bank (i.e. seed does not survive for more than one year) (Thompson and Grime 1979, Keeley 1977, Meney *et al.* 1994). Some species have both a transient and persistent component to their seed bank due to polymorphic seeds (Parker and Kelly 1989). These seed bank syndromes are largely limited to species capable of surviving fire by resprouting, with new individuals being recruited in the inter-fire period (Keeley 1977, Parker and Kelly 1989). Regional differences in seed bank syndromes, thus, reflect the different resident floras, environmental conditions, including type and intensity of predation, and fire regimes (Parker and Kelly 1989).

The knowledge of seed bank dynamics has implications for vegetation management. In many, varied vegetation types, seed banks are currently being exploited both to manage the composition and structure of existing vegetation, and to restore or establish native vegetation, both for conservation and economic purposes (Van der Valk and Pederson 1989). Models using seed bank information, together with information about reproductive characteristics and growth of species, have been developed for other vegetation types to predict recruitment after vegetation removal (e.g. Noble and Slatyer 1980, Van der Valk 1981). Often management of fynbos species is practiced without sensitivity of any of these factors.

Management for the most important goals in fynbos centers mainly on the application (or exclusion) of fire (Van Wilgen *et al.* 1992), through the use of controlled fires (Van Wilgen and Richardson 1985). If seed banks are transient then the season of fire, relative to the season of seed maturation and release is important (Le Maitre 1987, 1988). Fires in different seasons may ,thus, promote different species or growth forms, possibly promoting co-existence (Cowling 1987, Pierce and Cowling 1991b, Kilian and Cowling 1992). Fires commonly occur in fynbos in summer and autumn (Van Wilgen 1984) and this results in the recruitment of most fynbos species, including species with soil-stored seed banks (e.g. Bond 1984, Bond *et al.* 1984, Van Wilgen and Viviers 1985, Le Maitre 1987, 1988). Frequency of fire must also be placed into the context of seed bank development of species in fire-prone environments (Fox and Fox 1986). Several years may be needed before a species has produced enough seeds to establish a seed bank that will regenerate the species. Short interval fires may result in poor recruitment, as the seed banks have not accumulated much seed (Pierce 1987). For species whose seed germination is cued by fire, long-interval fires, that exceed plant life-spans, may result in populations being reliant on persistent seed banks for population replacement (Parker and Kelly 1989, Zedler and Zammit 1989).

The commercial harvesting of fynbos species, for cut-flowers and thatching reed, have become increasingly important veld-based industries in agriculturally marginal areas of the southern Cape lowlands and mountain foothills (Van Wilgen *et al.* 1992). The thatch industry based on the harvesting of tall Restionaceae, in particular, is rapidly growing and therefore, in addition to periodic fires, brushcutting is becoming a major disturbance factor in restioid fynbos types of the southern Cape lowlands (Bond 1984, Kruger and Bigalke 1984, Cowling *et al.* 1987b, Ball 1991). Effects of commercial harvesting include the removal of seed before maturation or removal of part of or all of the mature seed crop before incorporation into the seed bank. For species with transient seed banks, heavy harvesting in one year could deplete the seed banks. This could potentially result in local extinction of non-sprouting species if fire occurs before the species is able to recover and produce seed. The danger, therefore, exists that without management guidelines based on knowledge of the seed biology, the principle thatching reed species could potentially be overharvested. This could result in economic depletion, near extinction or actual extinction, as has been the case with other commercially important species (Lande *et al.* 1994). An analysis of seed banks, a study of the life histories and population responses to disturbance, of the two principle thatch species is a necessary starting point for understanding the vegetation dynamics, for designing and planning restioveld restoration, and to evaluate management techniques (Van der Valk and Pederson 1989). Comparative studies on the seed banks of undisturbed and disturbed areas are important in order to understand vegetation changes taking place, and many such studies have been undertaken for major disturbances such as logging, and agricultural and pastoral practices (Major and Pyott 1966, Thompson and Grime 1979, Archibold 1981).

This study aimed to determine soil seed bank size and persistence of the principle thatching reed species, *Thamnochortus insignis* and *Thamnochortus erectus* (Restionaceae). The study was conducted over two years, and emphasis was placed on examining and quantifying factors

influencing seed bank dynamics. A field experiment was carried out over one year to determine the effect of harvesting on all aspects of the seed bank dynamics of both species. This involved removing the current year's seed crop from approximately half of the two study sites by harvesting (i.e. brushcutting) and comparing the seed bank dynamics in this area to the unharvested area. This is one of the few experimental studies on seed bank dynamics (Leck *et al.* 1989). This study aims to compare the seed banks of two congeneric species and relate these findings to other life history attributes of the species. A "seed budget" (Mallik *et al.* 1984, Andersen 1989) was used to integrate the important processes influencing seed bank density. Implications for commercial harvesting of the study species on the seed banks dynamics are discussed. Guidelines for sustainable harvesting, based on sound ecological principles and an understanding of the biology, especially the seed bank ecology, and life history traits of the two species will be given.

The study addressed the following questions: (1) *Is there any annual variation in seed production or the size of the soil-stored seed banks?* (2) *Is there any evidence for seasonality in the seed banks?* (3) *How long do seeds remain viable in the soil (i.e. how persistent or transient are the seed banks)?* (4) *Are there any differences in seed banks of the two study species?* (5) *How does harvesting effect the above?* (6) *How do the seed bank characteristics relate to other life-history attributes and regeneration modes of the study species?*

In order to obtain answers to the above questions, both pre- and post-dispersal soil seed banks were estimated each year, using two methods, namely a physical separation technique, utilizing sieving and direct seed counts; and a seedling emergence technique. Both inputs and losses to the seed bank were studied, the latter being a process neglected in most seed bank studies (Cavers 1983, Fenner 1987). Seed production was monitored by bagging culms. Pre-dispersal seed predation was estimated by microscopic examination of seeds. Post-dispersal predation losses were determined experimentally by cafeteria experiments. Emergence,

persistence, or disappearance rates were determined, for each species, using two types of seed burial experiments, namely mesh bags and boxes.

2.3 STUDY SPECIES AND STUDY SITES

The restioids (herbaceous, rush-like perennials) *Thamnochortus insignis* and *Thamnochortus erectus* (Restionaceae) were selected for this study. A detailed description of the two study species can be found in Chapter 1 and their characteristics are summarized in Table 2.1. The fact that the species are both commercially harvested and differ in their regenerative mode after fire, contributed to their being chosen as study species. *Thamnochortus insignis* is an non-sprouter i.e. reproductively-mature plants are fire sensitive and regeneration is by soil-stored seed (Linder 1991). *Thamnochortus erectus* is a resprouter i.e. reproductively-mature plants survive fire by sprouting (Linder 1991). Both species recruit seedlings during inter-fire periods, as well as immediately after fire. Both species have winged, wind-dispersed seeds, with *T. insignis* and *T. erectus* seeds being dispersed from late autumn (mid-April) to mid-winter (July), and in summer (November to March), respectively. Seeds produced each year contribute to the soil-stored seed bank. *Thamnochortus insignis* and *T. erectus* seedlings germinate in late winter (from July to August) and from mid-autumn to mid-winter (April to June), respectively. The two allopatric species are closely related.

The field work was conducted at two study sites, namely Zoetendalsvallei (*T. insignis*: 34^0 44' 57"; 20^o 00' 9") and Zeekoeivlei (*T. erectus*: 34^0 39' 38"; 20^0 02' 35"), situated on the Agulhas Plain in the south western Cape, South Africa (Figure 2.1). Variation in microhabitat factors between study sites may effect the results of comparative studies of the kind undertaken in this study. As far as possible, an attempt was made to control these variables by limiting sampling to a small geographic region that was homogeneous in topography, soil type, drainage and time since the last fire. A detailed

description of the physiography, climate and floristics of the two study sites can be found in Chapter 1 and is summarized in Table 2.2.

Each study site comprised of a gently sloping (< 10°), homogeneous area of approximately 200 X 200 m, situated in a much larger area of similar vegetation. The study site was roughly divided in half, and five marked plots (10 X 10 m) were randomly located in each half (i.e. Area 1 and 2). One of these halves was randomly chosen and harvested, after the first seed dispersal period (1992) for both species. Plots in the unharvested area acted as controls for the harvested plots. An increase in the number of study sites for each species would have increased the generality of the results. In comparative seed bank studies, however, replication at many different study sites is prohibitive in terms of financial costs and time. It was also not possible to have plots interspersed in unharvested or harvested areas as this would occupy an undesirably (from the landowners point of view) large area. The experimental design, therefore, involved subsampling a given population rather than true replication. The study also included only one harvesting event for each of the study species.

Dry Restioid Fynbos, the vegetation type at both study sites, is tall, dense restioland (> 60% restioid cover) with a sparse shrub stratum (< 30%) (Campbell *et al.* 1981, Campbell 1985). Both study species are dominants at the respective study sites and their distribution was uniform across the local landscape. Both sites were free of alien vegetation. As is typical of fynbos vegetation, the study areas are subject to recurrent fires (Kruger 1984, Keeley 1986) usually in the dry summer and autumn months (Van Wilgen 1984). The vegetation community at the *T. insignis* site was 10 years old and that at the *T. erectus* site was more than 15 years old.

At the both sites, total projected foliage cover was approximately 80%, of which > 40% comprised *Thamnochortus* cover. At the *T. insignis* site, small- and large-leaved shrubs (non-proteoid) were common. Proteoids, graminoids (except the study species), forbs, geophytes, creepers, succulents and annuals were rare. At the *T. erectus* site, large-leaved non-proteoid shrubs

(dune thicket species) were common, as well as members of the Poaceae, which formed a dense field layer in places. Ericoid shrubs, other graminoids, forbs, geophytes, creepers, succulents and annuals were rare. Proteoids were absent.

The climate of the study area is typical of the south-western Cape, namely mediterranean-type with cool wet winters and warm dry summers. Climatic data for the nearest weather station (Cape Agulhas) are shown in Figure 2.2. The climate is mild, relatively uniform and frost free, with a mean annual temperature of 17°C (calculated for the period 1961-1993; Department of Environment Affairs, unpublished data). Approximately 65% of the 460 mm of annual precipitation falls in the winter months (May-October). During the year preceding and during the data collection period of this study (i.e. 1991-1993), annual rainfall was higher than the mean annual rainfall for two years (1992 = 527.5 mm; 1993 = 631 mm) and lower than the mean annual rainfall for one year (1991 = 408.9 mm). Mean monthly temperatures ranged from 24.0°C in January and 15.9°C in July during the same period. The area is extremely windy with mean daily winds, usually easterly in direction, exceeding 300 km day^{-1} during the summer months (Deacon *et al.* 1992).

The soils at both study sites were shallow (*ca.* 0.20-0.9 m), well-drained, structureless, grey colluvial sands (Fernwood form) of mixed origin (calcareous sands or Table Mountain Group sandstone) (Thwaites and Cowling 1988). The soils at the *T. erectus* site are older, browner in colour and finer in texture than those at the *T. insignis* site. The unconsolidated soil overlies Bredasdorp formation limestone and Table Mountain Group sandstone at the *T. insignis* and *T. erectus* sites, respectively. Soils at both sites were acidic.

2.4 METHODS AND MATERIALS

2.4.1 SEED CHARACTERISTICS

Seed mass (n = 200) was determined for both species using a Mettler AE 240 analytical balance. Seed long and short axis length (n = 50) and seed thickness (n = 50) were measured using a pair of SMIEC dial calipers (0-150 mm; 0.02 mm accuracy). Seeds were handled with forceps throughout.

For each species, paired t-tests (Zar 1984) were used to determine the significance of the effect of year on seed mass, seed long axis length, seed short axis length and seed thickness. For each of the two years, paired t-tests were used to determine the significance of the effect of species type on seed mass. The statistical computer programme, Statgraphics 6.0 (STSC Inc.) was used (Statgraphics 1987).

2.4.2 POPULATION STRUCTURE

Density (per m^2) of the study species, at each site, was calculated from counts of individuals in five randomly placed 10 x 10 m plots in harvested and unharvested vegetation, respectively. Estimates were made for two consecutive years, at the seed maturation stage. Juvenile plants were easily distinguishable from adult individuals by the absence of straight, unbranched culms. Counts were made of the number of adult female, male, other (sex undetermined) and dead individuals in each plot. The number and percentage of dead versus living individuals of each species, as well as individuals in the different sex categories were calculated. For each of the study species (*T. insignis*: 1992 n = 1697; 1993 n = 566 and *T. erectus*: 1992 n = 1028; 1993 n = 660]) plant height (height of the tallest current year's culm in cm) and tussock diameter (maximum diameter at ground level in mm) of all individuals in each plot were recorded. Difficulty was experienced in distinguishing between individual plants for *T. erectus*, because of the

lateral spreading habit. However, shallow excavations at the base were used to determine whether plants were separate or not.

For each year and each harvesting treatment, dispersion coefficients (variance : mean ratios) calculated from recorded population densities were used as an index of the degree of contagion (non-random distribution). In order to determine whether the total numbers of adult male and female individuals observed in five unharvested (i.e. Area 1), 10 x 10 m plots in 1992 and 1993 occurred in a frequency of 1 : 1, Chi-squared goodness of fit tests on observed versus expected plant data were conducted, for both species. Paired t-tests were used to determine the significance of the effect of year on plant height and tussock diameter. For each year and each harvesting treatment, paired t-tests were used to determine the significance of the effect of species type on plant height and tussock diameter. The statistical computer programme, Statgraphics 6.0 (STSC Inc.) was used for the t-tests (Statgraphics 1987).

The frequency of *T. insignis* and *T. erectus* live individuals (in both Area 1 and 2) observed in each of the plant height and tussock diameter categories and in each of the two years (i.e. 1992 and 1993) were arranged in contingency tables and analyzed using the chi-squared statistic. Plant height and tussock diameter categories were combined to prevent a biased chi-square value resulting from expected frequencies < 1 and/or expected frequencies < 5 in more than one-fifth of its cells. Chi-square analyses could not be preformed on dead adult plant tussock diameter data due to the low frequency of individuals in the tussock diameter categories. The statistical computer programme, Statgraphics 6.0 (STSC Inc.) was used for the chi-square analyses (Statgraphics 1987).

2.4.3 PRE-DISPERSAL SEED LOSSES

Seeds from a total of twenty randomly chosen culms (from those bagged for the seed production experiment in 1992 and 1993) of both species were sorted (using forceps and a dissecting microscope) and counted. Counts were made of intact plump (or filled) seed (i.e. endosperm present), aborted non-plump seed (i.e. no endosperm present) and predated seed (i.e. endosperm having been eaten by lepidopteran larvae and easily distinguished by larvae entrance and exit holes in the seed coat). Although all extensively deformed and shrivelled seed was classified as aborted, no tests were conducted to ascertain whether their appearance was a direct result of abortion, nor was their viability tested. The percentage of seeds in each category was calculated.

2.4.4 SEED PRODUCTION

Annual seed production of individuals of *T. insignis* and *T. erectus* was estimated at the study sites during 1992 and 1993. In 1993, seed production was estimated in both harvested (Area 1) and unharvested (Area 2) areas at both study sites. Both species had well-defined seed-production seasons (Table 2.1). The number of seeds produced per m^2 was determined by bagging parts of individual tussocks during the reproductive phenophase. Terylene netting bags were placed on culms of individuals to capture dispersed seed. The culms were bagged from immature seed stage until seed release. For each species and in each year, 200 baggings were replicated with two bags per plant and ten individuals per plot. However, a few replicates were lost due to rodent and wind damage. Seeds were sorted and counted in the laboratory using forceps. The species formed a seed coat regardless of whether or not the seed contents develop further and as a result plump seeds (assumed to be viable) were distinguished from empty seeds by applying light pressure to each seed. Inflorescence length and number of spiklets per inflorescence were determined for all bagged culms (n = 100 per treatment). The density of adult, female and male plants per m^2

was calculated (Section 2.4.2). Total number of current year's culms per female plant were estimated from counts from 200 randomly selected female plants, with 20 individuals per plot. Counts were made when the inflorescences were mature. Total number of current year's culms per m^2 was calculated from total number of culms per female plant multiplied by density of female individuals per m^2. The number of seeds produced per female individual was also estimated. This was calculated from mean number of culms per female plant multiplied by mean number of seeds per culm for each treatment and the total data set. Harvesting resulted in fewer than 20 female plants per plot. This necessitated the random removal of data points to obtain similar n values for comparison studies. The resulting seed production estimates etc. were similar to those obtained using the original full data set. Seed production was estimated as the number of plump seeds produced per m^2 ground surface area (assuming homogeneous seed dispersal). This was calculated from mean number of culms per m^2 multiplied by mean number of seeds per culm for each treatment and the total data set. The total (including plump, predated and aborted seed) annual seed production per m^2 was calculated using the percentage plump, aborted and predated data and annual plump seed production per m^2.

Three-way analysis of variance (ANOVA Type 1) (Zar 1984) was performed on inflorescence length (n = 200), number of spiklets per inflorescence (n = 200), and number of seeds per inflorescence (n = 200) in order to determine the influence of species, year and harvesting treatment on these variables. Number of spiklets per inflorescence and number of seeds per inflorescence counts were square root-transformed, after 0.5 was added to the counts (some of the data were small/zero counts). The statistical computer programme, Statgraphics 6.0 (STSC Inc.) was used (Statgraphics 1987).

2.4.5 POST-DISPERSAL SEED PREDATION

2.4.5.1 CAFETERIA EXPERIMENT

A cafeteria experiment was set up at the two study sites to quantify seed removals by ants and small mammals (rodents). Separate trials were run in May 1992 and March 1993 in an attempt to synchronize with the appropriate phenophase (i.e. seed release) for each study species (Table 2.1). A modified version of the methods of Auld (1986b) and Pierce and Cowling (1991b) was used.

Freshly released plump seeds of both species were harvested at each site from bags set up the day prior to the experiment. All seeds were handled with forceps to prevent contamination with human scent etc. Sites were randomly located in and near to each of the ten plots at each study site (to aid in rapid relocation). At each of these sites, four treatments were located: treatment 1 depots excluded invertebrates; treatment 2 excluded small mammals; treatment 3 was open to both invertebrates and small mammals and treatment 4 was closed to both. Depots with wire cages placed over petri dishes excluded small mammals. Depots comprising petri dishes with the sides coated in the commercial insect barrier Formex (Ciba-Geigy), excluded invertebrates (Bond and Breytenbach 1985). Depots accessible to invertebrates consisted of petri dishes fitted with gently sloping ramps to facilitate seed removal. Field densities of dispersed seed were estimated to ensure that the seed densities in the depots were not unnaturally high. Field densities for *T. insignis* were 163 seeds per 100 cm^2, and for *T. erectus* were 53 seeds per 100 cm^2. The depot seed densities (i.e. number of seeds per 63.62 cm^2) were lower: the *T. insignis* depots had 40 seeds $depot^{-1}$ and the *T. erectus* depots had 30 seeds $depot^{-1}$. Observations of seed removal by potential dispersal agents were made twice daily (morning and afternoon) over a period of four sunny, wind- and rain-free days. There was active insect and small mammal activity throughout the study period. At this time, any dispersal agents were identified or collected for future identification.

2.4.5.2 OBSERVATIONS

After completion of this experiment, it was evident that the seeds of both species were not removed by ants or by small mammals. Observations of seed loss from depots was only due to occasional gusts of wind. Subsequent field observations at both study sites led to the discovery that entire *T. insignis* culms were being removed from tussocks, presumably by small mammals (rodents). Evidence included diagonal serrated edges of culms remaining on the tussock and rodent tracks lined with inflorescences. An observation to quantify this form of mass seed removal was conducted at both sites at the end of the seed dispersal period. In 100 randomly located 1 X 1 m plots, counts were made of the total number of female and male plants, the number of male and female plants where there was evidence of culm removal, as well as the number of removed culms. The number of seeds lost in this way per cm^2 was calculated by multiplying the mean number of female culms removed per m^2 by the mean number of seeds per culm for each treatment and each study species.

2.4.6 SOIL SEED BANK SIZE AND DYNAMICS

Pre- and post-dispersal soil-stored seed banks of the study species, *T. insignis* and *T. erectus*, were estimated at one study site for each species in 1992 and 1993. At each sampling period, soil cores were randomly extracted from each of the ten randomly located plots at each of the two sites, using a cylindrical sampling tool (10 cm depth and 5 cm internal diameter; soil volume = 196.35 cm^3 and soil area = 19.63 cm^2 - see section 2.8 for calculations). for one year (1993), pre- and post-dispersal soil-stored seed banks of unharvested and harvested populations of the study species were estimated. Soil cores were taken in the five plots in each of two areas (i.e. Area 1 and 2) at each study site. As the study sites were relatively homogeneous in adult plant density and topography, a random sampling method was appropriate within the plots. The experimental design allowed

assessment of the local variability in seed bank sizes between plots and avoided results reflecting possible localized effects only.

For each year and each harvesting treatment, dispersion coefficients (variance : mean ratios) calculated from recorded direct seed counts (n = 300) and seedling counts were used as an index of the degree of contagion (non-random distribution) on a horizontal scale.

Generalised linear models (McCullagh and Nedler 1983) were fitted to the 1992 and 1993 pre- and post-dispersal and 1993 harvesting experiment seed bank (count) data (i.e. data from the pilot study, physical separation technique and seedling emergence technique) using the statistical package GLIM (Baker and Nedler 1978). This method avoids the assumptions of normality associated with many parametric procedures (Zar 1984). Log-linear models were fitted using Poisson error distributions and log link functions. Models were fitted separately for each of the two species and for pre- (i.e. Area 2) and post-harvesting (i.e. 1992) pilot study data. For the pre-harvesting data the effects of soil depth, season of sampling and year of sampling, as well as the interaction between these factors were noted. For the post-harvesting data the effects of soil depth, season of sampling and harvesting treatment, as well as the interaction between these factors were noted. Models were fitted separately for each of the two species and for pre- (i.e. Area 2) and post-harvesting (i.e. 1992) direct seed count data. For the pre-harvesting data the effects of season of sampling and year of sampling, as well as the interaction between these factors were noted. For the post-harvesting data the effects of season of sampling and harvesting treatment, as well as the interaction between these factors were noted. Models were fitted separately for pre- (i.e. Area 2) and post-harvesting (i.e. 1992) seedling count data. For the pre-harvesting data the effects of species type and year of sampling, as well as the interaction between these factors were noted. For the post-harvesting data the effects of species type and harvesting treatment, as well as the interaction between these factors were noted. Final models were selected using partial and marginal effects and with the use of

the Akaike (1974) criterion. Soil seed abundances are heterogeneous due to a variety of factors including dispersal (Major and Pyott 1966). In order to cope with this considerable variation in seed counts, the data were examined in terms of total number of seeds in 50 soil core samples for the pilot study data, in 150 soil core samples for the physical separation technique data and 10 soil core samples for the seedling emergence technique data. Where variation in the data were more than that described by Poisson distributions, the model was fitted using a scale factor (overdispersion parameter). In order to obtain a measurement of the percentage variation (P) in the data explained by the final model, the deviance (Dev) of the selected model was compared with the deviance of the model which contained only the mean using:

$$P = 100 \text{ X } (\text{Dev (mean only)} - \text{Dev (model)}) \div \text{Dev (mean only)}$$

where Dev (-) is the residual deviance (McCullagh and Nedler 1983).

2.4.6.1 PILOT STUDY

Many studies have shown that seed abundance decreases with soil depth (Auld 1986b, Bigwood and Inouye 1988), especially below 5 cm depth (Roberts 1981, Kilian 1991). In this study, soil-stored seed banks were sampled to a depth of 10 cm. The litter layer was included as it contained many seed (pers. obs.). It was assumed that seed bank densities declined greatly below a depth of 10 cm and that seeds buried at greater depths would not reach the soil surface for successful establishment. Hence it was assumed that this sampling depth should adequately reflect the seed store for potential recruitment. This assumption was tested by excavations and observations of seed germination depths of newly emerged seedlings at the study sites, as well by a pilot study of the distribution of seed in the soil profile. The pilot study was limited to ten pairs of soil samples per plot, taken at two depths (i.e. one soil core taken at each depth), namely to a depth of 10 cm below the soil surface (hereafter referred to as shallow soil

cores) and 10-20 cm below the soil surface (hereafter referred to as deep soil cores). Only two depths were used because of the difficulty in accurately differentiating a finer scale of soil depths in the unconsolidated soil. Sample bags were air dried for 24-72 hours before either immediately being processed or stored in dry conditions at room temperature until processing (in cases where there was a backlog of samples). Seeds were then separated from soil samples by sieving (500 μm aperture sieve) and scanning the remaining soil and litter (spread onto a white card) using tweezers and a dissecting microscope. Only seeds showing no external damage or disease were counted. The number of plump seeds per sample was determined. Seeds were tested for plumpness (assumed viability), by pressing the seed lightly with tweezers. Dissection of plump seeds confirmed that they contained a moist, white endosperm. Germination tests were not applied because the germination requirements of both species, and Restionaceae in general, are poorly understood (Singleton 1991), there were a great quantity of seeds needing testing and time constraints existed. Furthermore, usual *ex vitro* assessments of Restionaceae seed viability have been unsuccessful (see Meney and Dixon 1988). Tetrazolium tests (Grabe 1970, MacKay 1972, Moore 1985) were attempted, but seeds of both species did not stain readily (also see Meney *et al.* 1994). Because the data presented in this study are for plump or filled seeds and not viable seeds as such, the viable seed bank may have been overestimated. Data are reported as arithmetic means and standard deviations of 10 soil samples. Annual variation in seed bank densities at the two soil depths were expressed as seed numbers per sample, as well as seed numbers per m^2 and seed numbers per m^3 each year at each depth (given that 509.42 samples represent 1 m^2 of surface area and 5094.24 samples represent 1 m^3 of soil volume at the study sites - see section 2.8 for calculations).

2.4.6.2 PHYSICAL SEPARATION TECHNIQUE

Pre- and post-dispersal seed bank densities were determined from direct seed counts in 30 soil samples (30 X 3 combined soil cores = 90 soil cores in total) per plot. Three soil cores were thoroughly mixed and combined in a labelled brown paper bag in order to speed up the sieving and sorting process. The total volume and area sampled at each site at each sampling time was 177667 cm^2 (10 X (90 X 19.63 cm^2) and 176715 cm^3 (10 X (90 X 196.35 cm^3). Soil samples were air-dried, stored and processed in the same way as the pilot study samples were. Data are reported as arithmetic means and standard deviations of 150 soil samples. Annual variation in seed bank densities were expressed as seed numbers per sample, and converted to seed numbers per m^2 and seed numbers per m^3 each year (given that 169.78 samples represent 1 m^2 of surface area and 1698.08 samples represent 1 m^3 of soil volume at the study site - see section 2.8 for calculations).

2.4.6.3 SEEDLING EMERGENCE TECHNIQUE

The method of estimating the seed bank densities by direct seed counts was used together with a seedling emergence technique, to assess the accuracy of the former method. A further 30 (10 X 3 combined cores) soil cores were sampled in each of the ten plots at each of the sites before and after seed dispersal in 1992 and 1993. Owing to a shortage of controlled environment chamber space only ten samples, for each species, collected after dispersal each year could be used. Each soil sample was mixed (to maximize germination) and placed on the surface of separate pots of moistened, sieved soil collected from the study site (of the species concerned) in a controlled environment chamber. The filled pots were randomly placed in the chamber and rotated every week. Each sample was watered once daily (if dry) so that it was kept moist. The settings of the chamber were set at those similar to conditions experienced at the study sites during periods of peak germination [alternating 20°/10°C for 10/14 h light/dark, relative humidity 50% day

and 65% night (Department of Environmental Affairs, unpublished data, Appendix B)]. This method was used after a pilot study, conducted in a similar manner at an open greenhouse produced no results. Time, space and transport limitations also influenced the decision to conduct the experiment in the controlled environment chambers. For each set of samples, seedling emergence was monitored frequently (every second day) to assure that no plants emerged or died between censuses. No seeds germinated in the control pots of sieved soil. Once counted, the seedlings were tagged and labelled for the seedling growth experiment (Appendix C). A final census was undertaken after no seedling emergence was recorded for 14 days. Annual variation in germinable seed bank densities were expressed as seed numbers per sample, and converted to seed numbers per m^2 and seed numbers per m^3 each year (given that 169.78 samples represent 1 m^2 of surface area and 1698.08 samples represent 1 m^3 of soil volume at the study site - see section 2.8 for calculations).

The magnitude of the difference in soil-stored seed numbers estimated for each species and for each year, using the physical separation and seedling emergence techniques was calculated.

2.4.7 SEED STORAGE AND BURIAL

2.4.7.1 FIELD STUDY

To accurately quantify the age structure of the seed bank over an eighteen month study period, two different types of experimental seed banks were created in the field. The fate of seed in the seed bank was monitored at four month intervals during this period. Fresh seeds were collected from each of the study populations by bagging and shaking culms. Seeds were inspected and sorted to include only plump and intact seeds, and these were combined to form a bulk sample for each species for that year. Viability of plump seeds at release were assumed to be 100%. Soil used in the experimental seed banks was collected from the study sites, transported to

the laboratory, and sieved to remove any seeds. The soil collected from each site was used for the experimental seed banks at that site. The soil from each site was then mixed to ensure uniformity over all the experimental seed banks. Both burial boxes and burial bags were made of nylon mesh. The fine mesh size prevented immigration and emigration of the seeds of the study species. The material and cotton used were selected for their durability and porosity to both small soil fauna and soil moisture. It was assumed that the mico-environmental conditions of seed in the experimental seed banks was the same as for those seed outside such seed banks. Seeds could have one of four fates: persistence, predation, emergence, or disappearance due to death or removal. Because persistence was quantified using destructive harvesting of the seed banks, comparisons of the survivorship or emergence curves of seeds in the same seed bank was not possible. Data from all the experimental seed banks were used to quantify persistence, predation, emergence, or death of seed for each of the study species.

2.4.7.1 A) BURIAL BAG EXPERIMENT

Fifty *T. insignis* seeds and 25 *T. erectus* seeds were hand sorted and placed together with the soil in mesh bags (5 cm X 5 cm). The quantity of seed, of each species, placed in the bags was determined by the estimate of the density of seed per m^2 in the soil and the availability of seed. The bags were buried at 1 cm depth, in randomly chosen microsites, in both harvested and non-harvested plots, at the two study sites. Trials of the study species consisted of 200 (20 replicates in each of the 10 plots) burial bags. At approximately three months intervals, five replicate bags were randomly retrieved from the field and brought back to the laboratory. The contents of each mesh bag was removed and dried for 48 hours at room temperature in a brown paper bag. It was then sieved (500 μm aperture sieve) and the seeds and seedlings sorted and counted using forceps and a dissecting microscope. Five seed and seedling categories were distinguished, namely, intact seed, seed remains (seed center or wings), predated seed, germinated

seed (only radicle and/or plumule visible), and seedling. Intact seed and plump intact seed centers were grouped together to form the plump seed category. Germinated seed and seedlings were grouped together to form the germinated seed category. The percentage of the total seed in each category was calculated, as well as the percentage "lost" seed (i.e. seed that had disappeared due to death or removal).

2.4.7.1 B) BURIAL BOX EXPERIMENT

In order to determine whether seed deterioration and germination was influenced by the closed and buried nature of a bag, another experiment was set up which allowed seedlings to grow in an environment that was closer to field conditions. For each study species, seventy five replicate experimental seed banks were placed in a demarcated 100 m X 100 m area (to make recovery easier), shortly after seed dispersal in 1992. Experimental seed bank boxes (15 cm X 15 cm X 15 cm) were constructed of galvanized wire and nylon mesh. Boxes were buried at randomly located areas at the study sites, in such a way that at least 3 cm of the box protruded above the soil surface. Each box was filled with the same volume of prepared sand to the level of the surrounding soil, so as not to create a drainage depression or micro-watershed. Two hundred *T. insignis* and 100 *T. erectus* seeds were placed on the surface of the prepared sand and the top layers of sand lightly brushed over (as would normally happen by wind action). The amount of seed, of each species, placed in the boxes was determined by the estimate of the density of seed per m^2 in the soil and the availability of seed. The mesh lid of the enclosed box was securely sewn closed in the field, so as to prevent losses of seed from the boxes due to wind and animal activity, and prevent any new seed falling into the box. At approximately three months intervals, 15 replicate boxes were randomly retrieved from the field and brought back to the laboratory. The burial box samples were then dried and processed in the same way as the burial bag samples.

The Kolmogorov-Smirnov two-sample test (Siegel 1956) was used to determine differences in the cumulative distributions of seed survival and germination of *T. insignis* and *T. erectus* in both burial boxes (n = 15) and bags (n = 50) over time. The test for small samples was used on the burial box data (< 40 samples) and the test for large samples (> 40 samples) was used on the burial bag data. The Kolmogorov-Smirnov two-sample test (for small samples) was also used to determine differences in the cumulative distributions of seed survival and germination of the burial box and burial bag methods (n = 15) for both *T. insignis* and *T. erectus* over time. The statistical computer programme, Statgraphics 6.0 (STSC Inc.) was used (Statgraphics 1987).

2.4.7.2 LABORATORY STUDY

In addition to the burial of seed in experimental seed banks in the field, seeds collected from the same cohort were stored in brown paper bags in the laboratory at room temperature. Seed (n = 200) of each study species were selected for intact testa and plumpness (i.e. endosperm present) and 50 replicates were tested for the above criteria at three month intervals. This enabled a direct comparison to be made of seed stored in the laboratory with seed stored in the field and allowed determination whether overall seed deterioration with seed age was affected by environmental conditions experienced in the field.

2.4.8 SEEDLING DYNAMICS

Estimates of seedling gains (recruitment) and losses (mortalities) were based on measurements of the differences in recorded seedling densities between consecutive recording dates in harvested and unharvested mature vegetation. Seedlings of the study species were identified by comparing them with those regenerated under controlled environment chamber conditions from seed and soil samples taken at the study sites. One hundred randomly placed 1 X 1 m plots, in both the harvested and unharvested areas of both

study sites, were carefully searched for seedlings at the following times: *T. insignis* May 1992 (late autumn), August 1993 (late winter), November 1993 (early summer) and April 1994 (autumn); *T. erectus* December 1992 (summer), August 1993 (late winter) and April 1994 (autumn). Seedling height, basal diameter, number of culms, microsite and estimated year of germination were recorded. The different microsites identified included "open" vegetation, under fynbos vegetation (including *Thamnochortus* plants) and under newly harvested or discarded thatch. The number of seeds lost per m^2 due to germination was calculated.

For each year and each harvesting treatment, dispersion coefficients (variance : mean ratios) calculated from recorded seedling counts (n = 100) were used as an index of the degree of contagion (non-random distribution) on a 1 X 1 m horizontal and on a microhabitat scale, for both study species. For each year and each harvesting treatment, dispersion coefficients (variance : mean ratios) calculated from total recorded seedling counts at each sampling period (n = 4) were used as an index of the degree of contagion (non-random distribution) on a temporal scale, for both study species.

Generalised linear models (McCullagh and Nedler 1983) were fitted to the seedling (count) data using the statistical package GLIM (Baker and Nedler 1978). Log-linear models were fitted using Poisson error distributions and log link functions. Models were fitted separately for each of the two species and the effects of microhabitat, harvesting treatment and sampling period, as well as the interaction between these factors were noted. Final models were selected using partial and marginal effects and with the use of the Akaike (1974) criterion. Seedling abundances are heterogeneous due to a variety of factors including seed dispersal and seedling establishment (Major and Pyott 1966). In order to cope with this considerable variation in seedling counts the data were examined in terms of total number of seedlings in 100 1 X 1 m quadrats. Where variation in the data were more than that described by Poisson distributions, the model was fitted using a scale factor

(overdispersion parameter). In order to obtain a measurement of the percentage variation (P) in the data explained by the final model, the deviance (Dev) of the selected model was compared with the deviance of the model which contained only the mean using:

$$P = 100 \text{ X (Dev (mean only) - Dev (model)) } \div \text{ Dev (mean only)}$$

where Dev (-) is the residual deviance (McCullagh and Nedler 1983).

2.4.9 SEED BUDGET

A "seed budget" was constructed for comparison of estimates of numbers of plants or propagules per m^2 for *T. insignis* and *T. erectus* at different stages of their life cycles for both 1992 (unharvested vegetation) and 1993 (both unharvested and harvested vegetation), at both study sites. Estimates were from results presented in this chapter. Predicted and actual percentage plump seed loss and the difference between these two estimates were calculated for three time periods. These were from seed production to incorporation into the seed bank for 1992 and 1993, from incorporation of seed produced in 1992 into the seed bank to twelve months later, and from the 1992 seed production period to twelve months after incorporation of the same seed into the seed bank. For harvested vegetation, only predicted seed losses from the seed bank could be estimated as no seed bank estimates were available for 1994. Annual total seed production (total numbers of seed per m^2), for both 1992 and 1993, for both study species were calculated assuming constant ratios of aborted, predated and plump seed (using actual data from the study - Table 2.7) throughout both study areas at both study sites, in any one year. Seed loss due to whole culm removal was estimated assuming constant annual culm removal rates and plump seed production at both study sites. Seed losses to deep burial (Section 2.5.5), immediately after dispersal and incorporation into the seed bank, were calculated from the difference between estimates of number of seed per m^2 soil in post-dispersal and pre-dispersal deep seed bank estimates. Seed losses to deep

burial, from the time of incorporation into the soil seed bank to twelve months later, were calculated from the difference between estimates of number of seed per m^2 soil in 1992 post-dispersal and 1993 pre-dispersal deep soil cores. Both deep seed bank estimates for both study species include the current year's and older seed. The contribution of older seed to the net loss/gain of seed to deep soil can be considered to be negligible as less than 30% (*T. insignis*) and 7% (*T. erectus*) (assuming no loss of "old" seed with time, which is highly unlikely) of both seed bank estimates are made up of older seed. An increase in the estimates with time indicated a net increase in deeply buried seed and, therefore, loss of seed from the seed bank. A decrease in the deep seed bank estimates with time indicated a net decrease in deeply buried seed. This does not, however, indicate a gain to the potentially germinable soil seed bank, as seed decay etc. may be responsible for the net seed loss from deeply buried seed. Seed losses to burial in this scenario, therefore, cannot be estimated. Annual gains/losses to the seed bank (number of current year's plump seed per m^2), for both 1992 and 1993, and for both study species were calculated from the difference between post-dispersal (i.e. current year's seed and older seed) and pre-dispersal (i.e. seed older than current year's seed) seed bank estimates (Table 2.14). Predicted percentage loss of seed from the seed bank was calculated using data from both the burial box and burial bag experiments (Figure 2.6). Percentage actual seed loss, for both study species, with burial in the seed bank for twelve months were calculated from the difference between the current year's post-dispersal (i.e. current year's seed and older seed) and the following year's pre-dispersal (i.e. seed older than one year) seed bank estimates (Table 2.14). The contribution of seed older than the current year's seed is assumed to be negligible as it made up less than 6% (*T. insignis*) and 13% (*T. erectus*) of both seed bank estimates (assuming no loss of "old" seed with time, which is highly unlikely).

2.5 RESULTS

2.5.1 SEED CHARACTERISTICS

Average seed mass (x ± S.D., n = 200) for 1992 and 1993 was 1.017 ± 0.322 mg for *T. insignis* and 1.546 ± 0.555 mg for *T. erectus*. *Thamnochortus erectus* seeds were significantly greater (1.5 times) in seed mass than *T. insignis* seeds (1992: 1.8 times larger, $t = 15.7185$, $P < 0.001$; 1993: 1.3 times larger, $t = 7.42165$, $P < 0.001$) (Table 2.3). There was no common trend within years between both species. *Thamnochortus insignis* had a significantly greater seed mass in 1993 than in 1992 ($t = 7.29904$, $P < 0.001$). *Thamnochortus erectus* had a significantly greater seeds mass in 1992 than in 1993 ($t = 2.91565$, $P < 0.01$) (Table 2.3).

2.5.2 POPULATION STRUCTURE

Density

Mean data for five 10 X 10 m plots gave adult plant (reproductive and non-reproductive plants) densities (number of individuals per m^2) (x ± S.D.) for 1992 and 1993 of 1.23 ± 0.45 for *T. erectus* and 1.17 ± 0.56 for *T. insignis*. Average adult plant densities differed slightly between 1992 and 1993, although the trend was not the same for both species (Table 2.4). *Thamnochortus erectus* showed a small increase in density in 1993 compared to 1992 and *T. insignis* showed a small decrease in density in 1993 compared to 1992. Average reproductive adult plant densities were similar to those including non-reproductive adult plants, as "other" individuals were rare.

As would be expected with non-selective brushcutting (Section 1.4) the average adult plant density of both species decreased after harvesting (i.e. 1992 compared to 1993 in Area 1) (Table 2.4). The magnitude of decrease

was greater for *T. insignis* (21% decrease), than for *T. erectus* (9.6% decrease).

Living adult *T. insignis* plants (average variance to mean ratio for four sampling times = 4.59, n = 100) were observed to be far more clumped spatially, at the scale of 1 X 1 m, than *T. erectus* plants (average variance to mean ratio for three sampling times = 1.07, n = 100) (Whittaker 1975).

Sex and mortality category ratios

Thamnochortus erectus (609 individuals) had 1.04 times greater average total number of living adult plants in five, 10 X 10 m plots compared to *T. insignis* (584 individuals) in unharvested vegetation (i.e. Area 2) in 1992 and 1993. *Thamnochortus insignis*, however, had slightly more individuals than *T. erectus* in 1992 in unharvested vegetation, in both Area 1 (2.33 times greater) and Area 2 (1.09 times greater) (Table.2.4).

A count of the total dead versus living adult individuals in five, 10 X 10 m unharvested plots (i.e. Area 2) indicated that 0% (average for 1992 and 1993) of *T. insignis* individuals, and 0.32% (average for 1992 and 1993) were dead. Pre-harvesting (i.e. 1992) percentages of dead and live adult individuals of both species were uniform throughout the two study sites (i.e. comparison of Area 1 and 2) (Table.2.4).

After the harvesting (i.e. 1992 compared to 1993 in Area 1), the percentage of dead individuals increased slightly, in both species. The increase was greatest for *T. insignis*, compared to *T. erectus* (Table.2.4). Data were collected shortly after harvesting and the more detailed study on the effect of harvesting (Chapter 3) reveals longer-term changes in percentages of living and dead individuals.

A count of the total male, female and "other" adult individuals in five, 10 X 10 m plots indicated that percentages of individuals in each of the sex

categories for unharvested vegetation (i.e. Area 2) were similar for 1992 and 1993, for both species (Table.2.4). Pre-harvesting (i.e. 1992) percentages of male, female and other adult individuals of both species were uniform throughout the two study sites (i.e. comparison of Area 1 and 2) (Table.2.4). When non-reproductive individuals (i.e. "other") are excluded, , pre-harvesting (i.e. 1992) percentages of male and female adult individuals of both species are also uniform throughout the two study sites (i.e. comparison of Area 1 and 2) (Table.2.4). The unharvested *T. insignis* and *T. erectus* populations sampled (i.e. Area 2) in 1992 and 1993 did not exhibit a 1 : 1 ratio of male and female adult plants (*T. insignis* 1992: $X^2 = 7.23$, $P < 0.01$; *T. insignis* 1993: $X^2 = 5.17$, $P < 0.05$; *T. erectus* 1992: $X^2 = 22.98$, $P < 0.001$; *T. erectus* 1993: $X^2 = 30.168$, $P < 0.001$) (Table 2.5). There was a greater proportion of female than male adult plants in the populations sampled.

After the harvesting (i.e. 1992 compared to 1993 in Area 1), the percentage of "other" (non-reproductive) individuals increased to more than 50 percent of the total adult individuals, in both species (Table.2.4). The percentages of reproductive individuals (i.e. male and female individuals) increased considerably after harvesting, for both species (Table.2.4). These results are an expected direct result of culm removal with harvesting. When non-reproductive individuals are excluded, percentages of female adult individuals increased for both *T. insignis* and *T. erectus*, although the increase was slight for *T. insignis*. The harvested *T. insignis* and *T. erectus* populations sampled (i.e. Area 1) in 1993 did not exhibit a 1 : 1 ratio of male and female adult plants (*T. insignis*: $X^2 = 12.30$, *T. erectus*: $X^2 = 56.31$, $P < 0.001$) (Table 2.5). There were a greater proportion of female than male adult plants in the populations sampled.

Plant height

Thamnochortus insignis adult plants were significantly taller than *T. erectus* adult plants in unharvested vegetation (i.e. Area 2) for both years (1992: t =

12.8648, 1993: t = 19.4613, P < 0.001) (Table 2.6), although it was similar for both species in Area 1. Plant height was uniform across the entire study sites, for both species. (Table 2.6). Both species showed a significant increase in plant height with time (Area 2) (*T. insignis*: t = 10.8739, *T. erectus*: t = 4.27416, P < 0.001) (Table 2.6). Harvesting resulted in a decrease in plant height for both species, although the decrease was only significant for *T. erectus* (*T. insignis*: t = 1.88233, *T. erectus*: t = 8.12452, P < 0.001) (Table 2.6). After harvesting (i.e. 1992 compared to 1993 in Area 1), there was no significant difference between average adult plant heights of the species (1993: t = 0.470097) (Table 2.6). This was expected as harvesting is non-selective and both species are harvested at a similar height. Data were collected shortly after harvesting and thus species differences in culm growth rates were not detected.

The frequency distribution *T. insignis* and *T. erectus* individuals in the plant height categories showed a definite peak (Figure 2.3). For both species, in both areas and in both years, more than 32% of the total individuals were found in a single plant height category and more than 60% in two plant height categories. In 1992, however, the frequency of individuals in the various plant height categories in Area 1 was independent of species (X^2 = 3.42498, d.f. = 6), although in Area 2 it was not independent of species (X^2 = 143.695, d.f. = 6, P < 0.001) (Figure 2.3). In 1993 the frequency of individuals in the various plant height categories, in both unharvested and harvested vegetation, was not independent of species (Area 1: X^2 = 59.8939, d.f. = 6; Area 2: X^2 = 310.094, d.f. = 7; P < 0.001) (Figure 2.3).

Tussock diameter

Mean *T. erectus* living adult plant tussock diameters were significantly larger than those of *T. insignis* adult plants for both years and in both areas (1992 Area 1: t = 55.5581, 1992 Area 2: t = 39.6045, 1993 Area 1: t = 36.6713, 1993 Area 2: t = 22.5702, P < 0.001) (Table 2.6). Average *T. erectus* tussock diameters ranged from 2-5 times larger than those of *T. insignis*, for

unharvested plants. Tussock diameter was uniform across the entire study sites, for both species (Table 2.6). *Thamnochortus insignis* showed a significant increase in tussock diameter with time (Area 2) ($t = 10.5382$, $P < 0.001$). In contrast, *T. erectus* showed a significant decrease in tussock diameter with time (Area 2) ($t = 10.2493$, $P < 0.001$). The same significant trends were evident in Area 1 with time (*T. insignis*: $t = 12.8521$, *T. erectus*: $t = 4.55052$, $P < 0.001$). Harvesting (i.e. 1992 compared to 1993 in Area 1) resulted in a similar magnitude increase in tussock diameter for *T. insignis* and a similar magnitude decrease in tussock diameter for *T. erectus*, as was recorded in the unharvested area with time. The magnitude difference in post-harvesting average adult plant tussock diameters between *T. erectus* and *T. insignis* was within the range for unharvested plants. From these results, it is concluded that harvesting appears to have little effect on average adult plant tussock diameter for both species.

The frequency distribution of living individuals of both species in the tussock diameter categories showed a definite peak (Figure 2.4). In 1992 and 1993, however, the frequency of individuals in the various plant diameter categories, in both areas, was not independent of species (1992 Area 1: $X^2 = 736.379$, d.f. = 8; 1992 Area 2: $X^2 = 1292.68$, d.f. = 8; 1993 Area 1: $X^2 = 809.9510$, d.f. = 8; 1993 Area 2: $X^2 = 418.8730$, d.f. = 8; $P < 0.001$) (Figure 2.4).

The frequency of *T. insignis* and *T. erectus* dead individuals in the tussock diameter categories showed a definite clumping of individuals in two or more categories (Figure 2.5). Before harvesting, the majority of *T. erectus* dead individuals had small to medium tussock diameters. After harvesting, the majority of *T. insignis* dead individuals had small tussock diameters and the majority of *T. erectus* dead individuals had small to medium tussock diameters.

2.5.3 PRE-DISPERSAL SEED LOSSES

Number of plump, aborted and predated seeds per inflorescence

Average number of plump seeds per inflorescence (x ± S.D. (%), n = 20) for 1992 and 1993 was 361 ± 203 (93%) for *T. insignis* and 148 ± 84 (94%) for *T. erectus*. Average number of aborted seeds per inflorescence (x ± S.D., n = 20) for 1992 and 1993 was 7.18 ± 5.77 (2%) for *T. insignis* and 7.25 ± 11.61 (5%) for *T. erectus*. Average number of predated seeds per inflorescence (x ± S.D., n = 20) for 1992 and 1993 was 20.28 ± 15.41 (5%) for *T. insignis* and 1.2 ± 2.01 (1%) for *T. erectus*. The ratio of percentage plump, aborted and predated *T. insignis* seeds was was 46:1:1 (Area 1) and 62:1:3 (Area 2) for 1992 and 41:1:3 (Area 2) for 1993. Corresponding ratios for *T. erectus* were 90:5:1 and 212:15:1, and 91:3:1. The number of plump, aborted and predated seed per *T. insignis* and *T. erectus* inflorescence varied between years, with no consistent pattern between species or within species (Table 2.7). *Thamnochortus insignis* had a greater average number of plump seeds per inflorescence (approximately 2.43 times) compared to *T. erectus*, for both 1992 and 1993 (Table 2.7). The above trends were also evident in the estimation of seed production (Table 2.8). *Thamnochortus erectus* had a slightly greater average number of aborted seeds per inflorescence (approximately 1.01 times) compared to *T. insignis*, for both 1992 and 1993 (Table 2.7). *Thamnochortus insignis* had a greater average number of predated seeds per inflorescence (approximately 16.9 times) compared to *T. erectus*, for both 1992 and 1993 (Table 2.7). The number of plump, aborted and predated seeds per inflorescence was constant over the entire study site, for both species (Table 2.7).

Harvesting (i.e. 1992 compared to 1993 in Area 1) resulted in a decrease in the number of plump seeds per inflorescence and an increase in the number of aborted and predated seeds per inflorescence, in both species (Table 2.7). The ratio of percentage plump, aborted and predated seeds for the harvested area (i.e. Area 1 in 1993) was 7:1:2 for *T. insignis* and 9:3:1 for *T. erectus*.

Number of inflorescences per plant

In both species, inflorescences are confined to the current years' culms. Average number of current years' inflorescences per plant (x ± S.D., n = 100) for 1992 and 1993 was 59 ± 56 for *T. insignis* and 84 ± 67 for *T. erectus*. *Thamnochortus erectus* had a higher percentage of dead or senescent culms (i.e. not current years' culms) in the tussock (20-60%) at any point in time, compared to *T. insignis* (2-30%) (pers. obs.). The number of inflorescences per *T. insignis* and *T. erectus* plant varied greatly between 1992 and 1993, with no consistent pattern between species (Table 2.8). The number of inflorescences per plant was constant over the entire study site, for both species (Table 2.8).

Harvesting (i.e. 1992 compared to 1993 in Area 1) resulted in a decrease in number of current years' inflorescences per plant in both species (Table 2.8). After harvesting, the number of current years' inflorescences per plant decreased by 89.49% for *T. insignis* and 92.79% for *T. erectus*.

Number of spiklets per inflorescence

Average number of spiklets per inflorescence (x ± S.D., n = 100) for 1992 and 1993 was 8 ± 3 for *T. insignis* and 4 ± 1 for *T. erectus*. The number of spiklets per inflorescence was significantly less in both species in 1993 compared to 1992 ($F = 284.357$, $P < 0.001$) (Table 2.8 and 2.10). *Thamnochortus insignis* had a significantly greater average number of spiklets per inflorescence (approximately 2.30 times) compared to *T. erectus*, for both 1992 and 1993 ($F = 912.607$, $P < 0.001$) (Table 2.10), with the difference being related to both harvesting treatment and year. The interaction between species and year was also highly significant ($F = 38.818$, $P < 0.001$). The number of spiklets per inflorescence was constant over the entire study site, for both species (Table 2.8).

Harvesting (i.e. 1992 compared to 1993 in Area 1) resulted in a significant decrease in the number of spiklets per inflorescence in both species (P <

0.001) (Table 2.8 and 2.10). After harvesting, the number of spiklets per inflorescence decreased by 58.08% for *T. insignis* and 36.11% for *T. erectus*. The interaction between year and harvesting treatment ($F = 39.160$, $P < 0.001$) and species and year and harvesting treatment ($F = 33.068$; $P < 0.001$) was also highly significant. There was no interaction between species and harvesting treatment ($F = 0.004$).

Number of plump seeds per inflorescence

Average number of plump seeds per inflorescence ($x \pm$ S.D., $n = 100$) for 1992 and 1993 was 320 ± 174 for *T. insignis* and 148 ± 96 for *T. erectus*. These estimates were similar to those obtained in section 2.5.3 (Table 2.7). The number of plump seeds per inflorescence was significantly different in both species in 1993 compared to 1992 ($F = 276.168$, $P < 0.001$) (Table 2.8 and 2.11). *Thamnochortus insignis* had a significantly greater average number of plump seeds per inflorescence (approximately 2.16 times) compared to *T. erectus*, for both 1992 and 1993 ($F = 425.061$, $P < 0.001$) (Table 2.11). This difference is affected by both harvesting treatment and year. The number of plump seeds per inflorescence was constant over the entire study site, for both species (Table 2.8).

Harvesting (i.e. 1992 compared to 1993 in Area 1) resulted in a significant decrease in the number of plump seeds per inflorescence in both species ($F = 119.511$, $P < 0.001$) (Table 2.8 and 2.11). After harvesting, the number of plump seeds per inflorescence decreased by 73.72% for *T. insignis* and 75.82% for *T. erectus*. The interaction between year and harvesting treatment was also highly significant ($F = 182.736$, $P < 0.001$). There was no interaction between species and harvesting treatment ($F = 0.090$), and species and year and harvesting treatment ($F = 1.816$).

Number of plump seeds per plant

Average annual number of plump seeds per plant ($x \pm$ S.D., $n = 100$) for 1992 and 1993 was 19412 ± 9849 for *T. insignis* and 12489 ± 6250 for *T.*

erectus. The number of plump seeds per *T. insignis* and *T. erectus* plant varied greatly between 1992 and 1993, with no consistent pattern between the two species (Table 2.8). The annual number of plump seeds per plant was constant over the entire study site, for both species (Table 2.8).

Harvesting (i.e. 1992 compared to 1993 in Area 1) resulted in a decrease in annual number of plump seeds per plant in both species (Table 2.8). After harvesting, the annual number plump seeds per plant decreased by 97.24% for *T. insignis* and 98.26% for *T. erectus*.

Annual plump seed production

All bagged culms of both species produced plump seed. Both species produce considerable amounts of plump seed per m^2 (hereafter referred to as seed production). Average annual seed production per m^2 ($x \pm$ S.D., $n = 100$) for 1992 and 1993 was 12647 ± 3214 for *T. insignis* and 9205 ± 2192 for *T. erectus*. Annual seed production of *T. insignis* and *T. erectus* varied greatly between 1992 and 1993, with no consistent pattern between species (Table 2.8). *Thamnochortus insignis* had a greater average annual seed production per m^2 (approximately 1.37 times) compared to *T. erectus*, for both 1992 and 1993 (Table 2.8). The annual seed production per m^2 was constant over the entire study site, for both species (Table 2.8). *Thamnochortus erectus* seeds are significantly greater in seed mass than *T. insignis* seeds (approximately 1.5 times) (Table 2.3). When the difference in seed mass between species is taken into account, average annual seed production per m^2 for both 1992 and 1993 was approximately 1.13 times greater for *T. erectus* compared to *T. insignis* (Table 2.8).

Harvesting (i.e. 1992 compared to 1993 in Area 1) resulted in a drastic decrease in annual seed production in both species (Table 2.8). After harvesting, the annual seed production per m^2 decreased by 98.92% (*T. insignis*) and 98.87% (*T. erectus*). *Thamnochortus insignis* annual seed production per m^2 was 6.11 times larger than for *T. erectus*, after

harvesting. When the difference in seed mass between species is taken into account, annual seed production per m^2 was still larger for *T. insignis* than for *T. erectus*, after harvesting, although the magnitude difference decreased to 4.73 times. *Thamnochortus insignis* appears to have the ability to produce many reproductive culms immediately after harvesting, whereas *T. erectus* produces many more culms but most of these are non-reproductive.

Annual total seed production

Average annual total seed production per m^2 ($x \pm$ S.D., $n = 100$) for 1992 and 1993 was 13568 ± 3451 for *T. insignis* and 9683 ± 2296 for *T. erectus*. Annual total seed production for the two species in both areas and for both years followed similar patterns to annual plump seed production estimates. Annual total seed production of *T. insignis* and *T. erectus* varied greatly between the two years, with no consistent pattern between species (Table 2.8). *Thamnochortus insignis* had a greater average annual total seed production per m^2 (approximately 1.40 times) compared to *T. erectus*, for both 1992 and 1993 (Table 2.8). The annual total seed production per m^2 was constant over the entire study site, for both species (Table 2.8). *Thamnochortus erectus* seeds are significantly greater in seed mass than *T. insignis* seeds (approximately 1.5 times) (Table 2.3). When the difference in seed mass between species is taken into account, average annual seed production per m^2 for both 1992 and 1993 was approximately 1.08 times greater for *T. erectus* compared to *T. insignis* (Table 2.8).

Harvesting (i.e. 1992 compared to 1993 in Area 1) resulted in a predicted drastic decrease in annual total seed production in both species (Table 2.8). After harvesting, the annual total seed production per m^2 of decreased by 98.55% (*T. insignis*) and 98.46% (*T. erectus*). After harvesting, *T. insignis* annual total seed production per m^2 was 5.98 times larger than for *T. erectus*. When the difference in seed mass between species is taken into account, annual total seed production per m^2 was still larger for *T. insignis*

than for *T. erectus* after harvesting, although the magnitude difference decreased to 4.63 times.

2.5.5 POST-DISPERSAL SEED PREDATION

There appeared to be no seed losses by removal of individual seeds from both the control depots and all the other depots for both species i.e. there was no post dispersal seed predation of individual seeds (Table 2.12). No analyses were thus necessary to show that the individual seeds of neither species were dispersed or predated by both small mammals and ants. This was expected as seeds of neither species have an elaiosome which can act as an ant attractant, and the seeds were not large enough or easy to handle during transportation to a cache site to be a viable option for small mammals.

There was, however, small amounts of seed loss by whole culm removal and transportation to "unsafe sites" in *T. insignis*. No seed loss by whole culm removal and transportation for *T. erectus* were observed. The estimated average number of seed lost in this way was 84 seeds per m^2 (Area 1: 16 seeds per m^2, Area 2: 152 seeds per m^2). Many of the rodent nests dipped vertically down into the soil and consequently seed was buried deeply. It is predicted that even if the seed is not eaten by rodents, burial of seeds in nests is too deep for seeds to receive a stimulus to germinate in autumn conditions and during fires, and for seedlings to emerge successfully. These seeds are effectively lost from the seed bank unless relocation of seeds occur. There have, however, been no studies on germination and establishment of the study species from different soil depths. This seed loss will have no impact on recruitment given the enormous seed production in this species. *Rhabdomys pumilo* (Sparrmann) (striped field mouse) was the only rodent species recorded in the small-mammal survey at both study sites.

2.5.6 SOIL SEED BANK SIZE AND DYNAMICS

Pilot study

Seeds sieved from soil cores taken in both study populations before dispersal and the empirical field work done in this study (Section 2.4.6) indicate that a seed bank exists for both populations. Field observations indicated that no seedlings emerged from seeds buried at a soil depth of 10 cm or greater, justifying sampling only to this depth. Results from the pilot study indicated that there was a definite depth effect with the majority of seeds being found in the upper 10 cm of soil (Table 2.13). All further samples were consequently shallow in depth (i.e. 0-10 cm). Before dispersal, the average percentage *T. insignis* seed for unharvested vegetation in 1992 and 1993 was 86.92% in the shallow soil cores and 13.29% in the deep soil cores. After dispersal, the average percentage *T. insignis* seed for unharvested vegetation in 1992 and 1993 was 92.44% in the shallow soil cores and 7.56% in the deep soil cores. Corresponding values for *T. erectus* were 96.32% and 3.68%, and 91.48% and 8.52%. The percentage seed found in the shallow and deep soil cores in the unharvested area was similar for both 1992 and 1993, for both species (Table 2.13). Neither species showed consistently greater percentage seed in either of the two depth categories. After dispersal, *T. erectus*, however, showed a consistently lower percentage seed in the shallow soil cores, whereas *T. insignis* showed a consistently higher percentage of seeds in the shallow soil cores. Before dispersal (average data for Area 1 for 1992 and 1993), *T. erectus* had 1.11 times more seed than *T. insignis* in the shallow soil cores and *T. insignis* had 3.55 times greater percentage seed than *T. erectus* in the deep soil cores. After dispersal, however, *T. insignis* had 1.01 times more seed than *T. erectus* in the shallow soil cores and *T. erectus* had 1.13 times more seed than *T. erectus* in the deep soil cores.

The effects of depth, season and year were estimated for *T. insignis* and *T. erectus* data separately using a generalised linear model with a Poisson error

distribution and a log link function. For the *T. insignis* model there was significant depth, season and year effects, with no interactions. The final model explained 96% of the variation in the data (Pearsons Chi-squared for the model = 48.39; d.f. = 4; $P < 0.001$) (Section 2.9). Using the parameter estimates generated by GLIM, the expected average total number of seeds that would be found in 50 soil cores collected at two depths (i.e. shallow and deep), two sampling seasons (i.e. before and after dispersal) over two years (i.e. 1992 and 1993) was calculated (Section 2.9). The results indicate a depth decrease of 90.21% in the total numbers of seeds collected from deep compared to shallow soils. This finding held for both seasons and both years. The results indicate a seasonal increase of 581% in the total numbers of seeds collected from soils collected after dispersal compared to before dispersal. This finding held for both depths and both years. The results indicate an increase of 66% in the total numbers of seeds collected from soil in 1993 compared to 1992. This finding held for both depths and seasons. For the *T. erectus* model a scale factor of 91.47 was used, indicating considerable over-dispersion, possibly due to clumping of seeds. There was a significant depth effect and no season or year effect. The final model explained 74% of the variation in the data (Pearsons Chi-squared for the model = 2.10; d.f. = 6; $0.90 > P > 0.95$) (Section 2.9). Using the parameter estimates generated by GLIM, the expected average total number of seeds that would be found in 50 soil cores collected at two soil depths (i.e. shallow and deep) (Section 2.9). The results indicate a depth decrease of 93.24% in the total numbers of seeds collected from deep compared to shallow soils. This finding held for both seasons and both years.

Harvesting (i.e. 1992 compared to 1993 in Area 1) resulted in an increase in percentage seed in the pre-dispersal shallow soil cores and a decrease in percentage seed in the post-dispersal shallow soil cores, for both species (Table 2.13). After harvesting, the percentage *T. insignis* seed in the pre-dispersal shallow soil cores was 1.49 times greater. The percentage *T. erectus* seed in the pre- and post-harvesting pre-dispersal shallow soil cores was similar. After harvesting, the percentage seed in the pre-dispersal deep

soil cores was 6.14 (*T. insignis*) and 1.06 (*T. erectus*) times less. After harvesting, the percentage seed in the post-dispersal shallow soil cores were 1.14 (*T. insignis*) and 1.24 (*T. erectus*) times less. After harvesting, the percentage seed in the post-dispersal deep soil cores were 3.94 (*T. insignis*) and 2.27 (*T. erectus*) times greater.

The effects of depth, season and harvesting treatment were estimated for *T. insignis* and *T. erectus* data separately using a generalised linear model with a Poisson error distribution and a log link function. For the *T. insignis* model there were depth, season and harvesting treatment effects, with no interactions. The final model explained 99% of the variation in the data (Pearsons Chi-squared for the model = 4.68; d.f. = 4; $0.25 > P > 0.50$) (Section 2.9). Using the parameter estimates generated by GLIM, the expected average total number of seeds that would be found in 50 soil cores collected at two depths (i.e. shallow and deep), two seasons (i.e. before and after dispersal) and in harvested and unharvested vegetation was calculated (Section 2.9). The results indicate a depth decrease of 85% in the total numbers of seeds collected from deep compared to shallow soils. This finding held for both seasons and both harvesting treatments. The results indicate a seasonal increase of 392% in the total numbers of seeds collected from soils collected after dispersal compared to before dispersal. This finding held for both depths and both harvesting treatments. The results reflect an increase of 99% in the total numbers of seeds collected from soil in unharvested vegetation compared to harvested vegetation. This finding held for both depths and both seasons. For the *T. erectus* model a scale factor of 90.89 was used, indicating considerable over-dispersion, possibly due to the clumping of seeds. There was a depth effect, and no season and harvesting treatment effects. The final model explained 80% of the variation in the data (Pearsons Chi-squared for the model = 1.71; d.f. = 6; $0.90 > P > 0.95$) (Section 2.9). Using the parameter estimates generated by GLIM, the expected average total number of seeds that would be found in 50 soil cores collected at two depths (i.e. shallow and deep) was calculated (Section 2.9). The results indicate a depth decrease of 92% in the total numbers of seeds

collected from deep compared to shallow soils. This finding held for both seasons and both harvesting treatments.

Physical separation technique (i.e. direct seed counts)

Average annual pre-dispersal seed bank size (mean number of plump seeds per m^2) ($x \pm$ S.D., n = 150) for 1992 and 1993 was 1633.30 ± 2601.35 for *T. insignis* and 1133.55 ± 2643.65 for *T. erectus*. Average annual post-dispersal seed bank size per m^2 ($x \pm$ S.D., n = 150) for 1992 and 1993 was 3773.05 ± 6026.50 for *T. insignis* and 2530.30 ± 3482.30 for *T. erectus*. *Thamnochortus insignis* had a greater average annual pre- (1.44 times) and post-dispersal (1.49 times) seed bank size compared to *T. erectus* for 1992 and 1993 (Table 2.14). The annual pre-dispersal seed bank size per m^2 of *T. erectus* was 1.54 times greater than that of *T. insignis* in 1992, although that of *T. insignis* was 1.57 times greater than that of *T. erectus* in 1993. The annual post-dispersal seed bank size per m^2 of *T. insignis* was 1.35 (1992) and 1.64 (1993) times greater than that of *T. erectus*..

Thamnochortus erectus seeds are significantly greater in seed mass than *T. insignis* seeds (approximately 1.5 times) (Table 2.3). When the difference in seed mass between species is taken into account, average annual pre- (1.06 times) and post-dispersal (1.02 times) seed bank size per m^2 for both 1992 and 1993 was greater for *T. erectus* compared to *T. insignis* (Table 2.14).

Seed bank size for *T. insignis* and *T. erectus* varied greatly between the two years. Patterns were consistent for *T. insignis* and inconsistent for *T. erectus* (Table 2.14). Both *T. insignis* or *T. erectus* showed increments in pre-dispersal seed densities over the two years. Only *T. insignis* showed an increment in post-dispersal seed density over the two years. Annual differences in pre-dispersal seed bank size (mean number of seed per m^2) ranged from 208 (1992) to 3058 (1993) seeds per m^2 for *T. insignis* and from 321 (1992) to 1946 (1993) seeds per m^2 for *T. erectus*. Annual differences in post-dispersal seed bank size (mean number of seed per m^2) ranged from

3481 (1992) to 4066 (1993) seeds per m^2 for *T. insignis* and from 2474 (1993) to 2586 (1993) seeds per m^2 for *T. erectus*. The annual pre-dispersal seed bank size per m^2 was 1368.22% (*T. insignis*) and 505.38% (*T. erectus*) greater in 1993 compared to 1992 (Table 2.14). The annual post-dispersal seed bank size per m^2 was 16.81% greater (*T. insignis*) and 4.33% (*T. erectus*) less in 1993 compared to 1992 (Table 2.14).

As was expected, seed bank size was highly variable between seasons in both species (Table 2.14). Seeds of *T. insignis* and *T. erectus* are dispersed and either lie on the soil surface or become buried in the soil, and remain dormant through the summer. Those seeds that survive to the following autumn either germinate and emerge, persist (enter the seed bank), or die. Annual seed bank size per m^2 was greater after dispersal compared to before dispersal, for both species and both years (Table 2.14). Annual seed gain to the soil seed bank can be estimated by calculating the difference between post-dispersal and pre-dispersal seed bank size in any one year (Section 2.5.9). Average annual post-dispersal seed bank size per m^2, for both years, was 2.31 (*T. insignis*) and 2.23 (*T. erectus*) times greater than pre-dispersal seed bank size. *Thamnochortus insignis* post-dispersal seed bank size per m^2 was 16.71 (1992) and 1.33 (1993) times greater than pre-dispersal seed bank size. *Thamnochortus erectus* post-dispersal seed bank size per m^2 was 8.05 (1992) and 1.27 (1993) times greater than pre-dispersal seed bank size.

The effects of year and season were estimated for *T. insignis* and *T. erectus* data separately using a generalised linear model with a Poisson error distribution and a log link function. For the *T. insignis* model there was significant year and season effects, with no interactions. The final model explained 60% of the variation in the data (Pearsons Chi-squared for the model = 1414.00; d.f. = 1; $P < 0.001$) (Section 2.9). Using the parameter estimates generated by GLIM, the expected average total number of seeds that would be found in 150 soil cores collected at two seasons (i.e. before and after harvesting) over two years (i.e. 1992 and 1993) was calculated

(Section 2.9). The results indicate a seasonal increase of 131% in the total numbers of seeds collected from soils collected after dispersal compared to before dispersal. This finding held for both years. The results reflect an increase of 93% in the total numbers of seeds collected from soil in 1993 compared to 1992. This finding held for both sampling seasons. For the *T. erectus* model there was significant year and season effects, with no interactions. The final model explained 59% of the variation in the data (Pearsons Chi-squared for the model = 788.00; d.f. = 1; $P < 0.001$) (Section 2.9). Using the parameter estimates generated by GLIM, the expected average total number of seeds that would be found in 150 soil cores collected at two seasons (i.e. before and after harvesting) over two years (i.e. 1992 and 1993) was calculated (Section 2.9). These results indicate a seasonal increase of 123% in the total numbers of seeds collected from soils collected after dispersal compared to before dispersal. This finding held for both years. The results reflect an increase of 52% in the total numbers of seeds collected from soil in 1993 compared to 1992. This finding held for both seasons.

A Spearman rank correlation of post-dispersal seed bank size versus seed input for each of the ten plots for both species in both 1992 and 1993 yielded the following results. For *T. insignis* there was a non-significant positive relationship ($r_S = 0.2121$, n = 10) in 1992 and a significant positive relationship ($r_S = 0.8182$, $P < 0.01$, n = 10) in 1993. For *T. erectus* there was no relationship ($r_S = - 0.0424$, n = 10) in 1992 and a significant positive relationship ($r_S = 0.7212$, $P < 0.05$, n = 10) in 1993. Annual *T. insignis* seed production (Area 2) exceeded post-dispersal seed bank size by 4.98 times in 1992 and 1.95 times in 1993. Annual seed production in *T. erectus* (Area 2) exceeded post-dispersal seed bank size by 2.19 times in 1992 and 5.16 times in 1993 (Table 2.8 and 2.14).

Annual pre-and post-dispersal seed bank size per m^2 for both species differed slightly over the study site for both species (Table 2.14).

Seed numbers per sample were highly variable at all sampling times and for both species. This is indicated by the high values of the standard deviation of the mean (n = 150 soil samples) (Table 2.14). In 1992, pre-dispersal seed numbers per sample ranged from 0 to 22 for both species. In 1992, post-dispersal seed numbers per sample ranged from 0 to 290 for *T. insignis* and from 0 to 213 for *T. erectus*. In 1993, pre-dispersal seed numbers per sample ranged from 0 to 257 for *T. insignis* and from 0 to 134 for *T. erectus*. Corresponding values for the 1993 data were 0 to 356 and 0 to 109.

Harvesting (i.e. 1992 compared to 1993 in Area 1) resulted in an increase in pre-dispersal and a decrease in post-dispersal seed bank size per m^2 for both species (Table 2.14). After harvesting, the annual pre-dispersal seed bank size per m^2 increased by 2957.03% for *T. insignis* and 56.35% for *T. erectus*. After harvesting, the annual post-dispersal seed bank size per m^2 decreased by 45.39% for *T. insignis* and 85.38% for *T. erectus*. After harvesting, annual pre- (1.22 times) and post-dispersal (3.23 times) seed bank size per m^2 was greater for *T. insignis* compared to *T. erectus*. When the difference in seed mass between species is taken into account, annual pre-dispersal seed bank size per m^2 was larger for *T. erectus* than for *T. insignis* after harvesting, although the magnitude difference was 1.06 times. Annual post-dispersal seed bank size per m^2 was still larger for *T. insignis* than for *T. erectus* after harvesting, although the magnitude difference decreased to 2.50 times. For both species the dispersal effect was not clear after harvesting. Annual pre-dispersal seed bank size per m^2 was less than post-dispersal seed bank size for *T. insignis* (1.10 times) and *T. erectus* (2.92 times).

The effects of harvesting treatment and season were estimated for *T. insignis* and *T. erectus* data separately using a generalised linear model with a Poisson error distribution and a log link function. A scale factor of 65.05 was used for the *T. insignis* model, indicating considerable over-dispersion, possibly due to the clumping of seeds. The model, which included harvesting treatment effect only (Pearsons Chi-squared for the model =

and no interactions.

2.021; d.f. = 2; 0.25 > P > 0.50), no season effect (The final model explained 92% of the variation in the data (Section 2.9). Using the parameter estimates generated by GLIM, the expected average total number of seeds that would be found in 150 soil cores collected in harvested and unharvested vegetation was calculated (Section 2.9). The results reflect an increase of 145% in the total numbers of seeds collected from soil in unharvested vegetation compared to harvested vegetation. This finding held for both seasons. For the *T. erectus* model there was significant harvesting and season effects, with no interactions. The final model explained 73% of the variation in the data (Pearsons Chi-squared for the model = 400.8; d.f. = 1; P < 0.001) (Section 2.9). Using the parameter estimates generated by GLIM, the expected average total number of seeds that would be found in 150 soil cores collected at two seasons (i.e. before and after dispersal) in harvested and unharvested vegetation was calculated (Section 2.9). These results indicate a seasonal decrease of 9% in the total numbers of seeds collected from soils collected after dispersal compared to before dispersal. This finding held for both harvesting treatments. The results reflect an increase of 163% in the total numbers of seeds collected from soil in unharvested vegetation compared to harvested vegetation. This finding held for both seasons.

Seedling emergence technique (i.e. seedling counts)

Thamnochortus insignis had a greater average annual post-dispersal seed bank size compared to *T. erectus*, for both 1992 and 1993 (Table 2.15). Average annual post-dispersal seed bank size per m^2 ($x \pm$ S.D., n = 10) for 1992 and 1993 was 1044.3 ± 1177.45 for *T. insignis* and 764.15 ± 596.0 for and *T. erectus*. The magnitude difference in the average annual post-dispersal seed bank size per m^2 for the two species was 1.37 times (Table 2.15). The annual post-dispersal seed bank size per m^2 of *T. insignis* was 1.43 (1992) and 1.31 (1993) times greater than that of *T. erectus*.

Thamnochortus erectus seeds are significantly greater in seed mass than *T. insignis* seeds (approximately 1.5 times) (Table 2.3). When the difference in seed mass between species is taken into account, average annual post-dispersal seed bank size per m^2 for both 1992 and 1993 was approximately 1.37 times greater for *T. erectus* compared to *T. insignis* (Table 2.15).

Post-dispersal seed bank size per m^2 for *T. insignis* and *T. erectus* varied slightly between the two years. Both species showed increments in post-dispersal seed densities over two years (Table 2.15). Annual differences in post-dispersal seed bank size per m^2 ranged from 1019 (1992) to 1070 (1993) seeds per m^2 for *T. insignis* and from 713 (1992) to 815 (1993) seeds per m^2 for *T. erectus*. The annual post-dispersal seed bank size per m^2 was 5.01% (*T. insignis*) and 14.29% (*T. erectus*) greater in 1993 compared to 1992 (Table 2.15).

The effects of species and year were estimated using a generalised linear model with a Poisson error distribution and a log link function. There were no significant species and year effects and no interactions, and the data are best explained by the null model or the mean.

Annual *T. insignis* seed production (Area 2) exceeded post-dispersal seed bank size by 17.02 times in 1992 and 7.43 times in 1993. Annual *T. erectus* seed production (Area 2) exceeded post-dispersal seed bank size by 7.93 times in 1992 and 15.65 times in 1993 (Table 2.8 and 2.15).

The annual post-dispersal seed bank size per m^2 was variable over the study site for both species (Table 2.15).

Seed numbers per sample of both species were variable at all sampling times. This is indicated by the high values of the standard deviation of the mean (n = 10 soil samples) (Table 2.15). In 1992, post-dispersal seedling numbers per sample ranged from 0 to 18 for *T. insignis* and from 0 to 9 for

T. erectus. In 1993, post-dispersal seedling numbers per sample ranged from 0 to 21 for *T. insignis* and from 0 to 12 for *T. erectus*.

Harvesting (i.e. 1992 compared to 1993 in Area 1) resulted in a decrease in post-dispersal seed bank size per m^2 for both species (Table 2.15). Harvesting resulted in a 60% (*T. insignis*) and 80.02% (*T. erectus*) decrease in the annual post-dispersal seed bank size per m^2. After harvesting (i.e. 1993, Area 1), annual post-dispersal seed bank size per m^2 was 2 times greater for *T. insignis* compared to *T. erectus*. When the difference in seed mass between species is taken into account, annual post-dispersal seed bank size per m^2 for 1993 was still larger for *T. insignis* than for *T. erectus*, although the magnitude difference decreased to 1.55 times.

The effects of harvesting treatment and species were estimated using a generalised linear model with a Poisson error distribution and a log link function. The model, which included harvesting treatment effect only (Pearsons Chi-squared for the model = 1.01; d.f. = 2; $0.50 > P > 0.75$), indicated that there was no species effect and no interactions. The final model explained 97% of the variation in the data (Section 2.9). Using the parameter estimates generated by GLIM, the expected average total number of seeds that would be found in 10 soil cores collected in harvested and unharvested vegetation was calculated (Section 2.9). These results indicate a harvesting increase of 1133% in the total numbers of seeds collected from soils collected in unharvested vegetation compared to harvested vegetation. This finding held for both species.

Comparison of methods: seed counts versus germinant counts

Comparisons of physical separation and seedling emergence techniques as different methods of determining seed bank size showed significant differences for both species and at all sampling times (Table 2.14 and 2.15). Only post-dispersal estimates of seed bank size using the seedling emergence method were made, thus, comparisons between the estimates

obtained using the two methods could unfortunately not be made for pre-dispersal data. The seedling emergence method showed consistently lower seed bank estimates compared to the physical separation method for both species (Table 2.14 and 2.15). Average magnitude difference between the two methods, in unharvested vegetation (i.e. Area 2), for 1992 and 1993 post-dispersal data, was 3.61 times for *T. insignis* and 3.34 times for *T. erectus*. The magnitude difference between the seed bank estimates using the two methods were similar for 1992 and 1993 estimates, for both species. For *T. insignis*, the magnitude difference between estimates were between 3.42 (1992) and 3.80 (1993) times; the range for *T. erectus* were between 3.04 (1993) and 3.63 (1992) times. The magnitude differences between the seed bank estimates using the two methods were not the same throughout the study sites or for both species (Table 2.14 and 2.15).

Harvesting (i.e. 1992 compared to 1993 in Area 1) resulted in an increase in the magnitude difference between the two methods for *T. insignis*, and a decrease in the magnitude difference between the two methods for *T. erectus* (Table 2.14 and 2.15). The magnitude difference between the two methods for *T. insignis* was 9.97 (1992) and 13.61 (1993) times, and for *T. erectus* was 11.52 (1992) and 8.82 (1993) times.

The coefficients of variation (i.e. variance to mean ratios, n = 150) were high (i.e. > 1) for the physical separation technique, for both species; and the seedling emergence technique for *T. insignis*, at all sampling times (Table 2.16). This suggests that within these seed banks, the seeds are highly clumped (Whittaker 1975, Zar 1984). The coefficients of variation for *T. erectus* for the seedling emergence method were 1 or less than one, suggesting an even dispersion of readily germinable seeds within the seed bank (Table 2.16) (Whittaker 1975, Zar 1984). For *T. insignis*, the post-dispersal variance to mean ratios for the seed bank estimates using the physical separation method were greater than the pre-dispersal estimates, irrespective of year or study area. This was also the case for *T. erectus* seed bank estimates in 1992, but the variance to mean ratios were greater before

dispersal in 1993. Variance to mean ratios were consistently greater for the physical separation method compared to the seedling emergence method, for both species. No pre-dispersal variance to mean ratios were available for the seedling emergence method. For *T. insignis*, the magnitude difference in the variance to mean ratios for the two methods ranged from 17.25 (1993) to 28.05 (1992) times; the range for *T. erectus* was 17.21 (1993) to 50.16 times. The high variability of seed numbers per sample for both techniques, at all sampling times and for both species was also indicated by the high values of the standard deviation of the mean. A greater variability was evident for the physical separation technique for both species. Harvesting resulted in an increase in the variance to mean ratios for *T. insignis* for both techniques. Similar pre- and post-harvesting variance to mean ratios were calculated for *T. erectus* for both techniques.

The number of seeds germinating from the soil samples were used as an estimate of the minimum viable number of seeds in the soil, at any period in time. They were compared to the number of plump seeds counted in the same volume of soil collected at the same time. This gave an average viability of plump seeds for both 1992 and 1993 to be 27.80% (1992: 29.28%, 1993: 26.32%) for *T. insignis* and 30.25% (1992: 27.57%, 1993: 32.93%) for *T. erectus*.

2.5.7 SEED STORAGE AND BURIAL

Seed deterioration during storage of fresh plump *T. insignis* and *T. erectus* seeds (produced in 1992) in both in the laboratory and in two types of experimental soil seed banks in the field was investigated for a total of 16/18 months at approximately four month intervals.

There was no deterioration after 18 months storage in the laboratory for both *T. insignis* and *T. erectus* (i.e. both species showed 100% plumpness after storage).

Deterioration after 16/18 months burial at approximately 10 mm depth in the field, differed between species and experimental seed bank type (Figure 2.6). The percentage of remaining plump seeds were as follows (mean ± S.D.): *T. insignis*, 60.40 ± 13.55 (n = 15 boxes) and 88.22 ± 10.73 (n = 25 bags) and *T. erectus*, 80.87 ± 5.72 (n = 15 boxes) and 90.32 ± 11.17 (n = 25 bags). Both species had persistent seed banks, although those of *T. erectus* were more persistent than those of *T. insignis*. As seeds were only tested for plumpness and not viability as such, the viability of buried seed of both species may be overestimated.

Seeds are lost from the soil seed bank both by predation, successful germination and emergence (i.e. seedlings), and by failed germination, seed death and subsequent decay, seed emigration (either passive or active removal) and deep burial. Burial in "closed" experimental seed banks did not allow immigration/emigration or burial of seed to take place. All the other types of seed loss occurring during burial could, however, be estimated using this method. Successful and failed germination were grouped together to form the germinated seed category. Seed loss to early failed germination or seed decay could not always be distinguished, and were grouped together to form the "lost" seed category. Experimental seed bank losses were apparent for both species, although seed losses were higher for *T. insignis* compared to *T. erectus* over the 16/18 month study period (Figure 2.6). The percentage of persistent seed (i.e. remained plump and intact) of both species decreased with burial time and the percentage of lost seed (i.e. predated, germinated and "lost" seed categories) increased accordingly (Figure 2.6).

From these results one can make some general observations regarding differences in seed persistence and loss, with regard to species type and method of burial (Figure 2.6). *Thamnochortus erectus* showed greater seed persistence than *T. insignis* for both methods of burial (Figure 2.6). After 16 months burial, the average difference in percentage seed persistence for both burial boxes and bags was 1.20 times. *Thamnochortus insignis* showed

greater seed losses (for all categories) than *T. erectus* for both methods of burial. After 16 months burial, the average difference in percentage seed loss for both burial boxes and bags was 3.25 times. More specifically, after 16 months of burial, the average difference was 3.23 (predated), 1.98 (germinated) and 4.38 ("lost") times.

Burial bags showed greater seed persistence and burial boxes showed greater seed loss (all categories combined) during the study period, for both species (Figure 2.6). After 16 months of burial, the magnitude difference in seed persistence for the two methods of seed burial was 1.43 times for *T. insignis* and 1.1 times for *T. erectus*. After 16 months of burial, the magnitude difference in seed loss for the two methods of seed burial was 2.10 times for *T. insignis* and 3.02 times for *T. erectus*. When the seed loss categories were examined separately for both species, seed loss was highest for burial bags for predated and germinated seed categories and highest for burial boxes for the "lost" seed category. After 16 months of burial, the average difference was 1.42, 3.84 and 5.45 times for *T. insignis* predated, germinated and "lost" seed, respectively. After 16 months of burial, the average difference was 1.82, 10.23 and 1.13 times for *T. erectus* predated, germinated and "lost" seed, respectively. Overall, the burial boxes provided an environment for buried seeds that is closer to that experienced by seeds naturally buried in the seed bank. Burial boxes are, however, more easily damaged by animals (especially domestic animals such as cattle) than burial bags.

For both species, there was a large reduction in the percentage of persistent seed between 4 and 8 months of burial, corresponding to an increase in the percentage of "lost" seed (Figure 2.6). Percentage *T. insignis* seed loss by germination and predation increased dramatically between 8 and 12 months of seed burial for both methods of burial. Percentage *T. erectus* seed loss by germination increased dramatically between 8 and 12 months of seed burial for burial boxes only.

Using mean seed numbers, experimental seed bank dynamics of both species can be summarized by plotting seed persistence and emergence as a function of time (Figure 2.7) for each of the two methods. Cumulative survival of both *T. insignis* and *T. erectus* seed in time in burial boxes and bags do not follow the same distribution pattern (*T. insignis*: $K_D = 24.13$, $N = 15$, *T. erectus*: $K_D = 10.86$, $N = 15$; $P < 0.01$) (Figure 2.7 and Table 2.17). Cumulative germination of both *T. insignis* and *T. erectus* seed in time in burial boxes and bags do not follow the same distribution pattern and the difference is greater for *T. insignis* ($K_D = 12.03$, $N = 15$, $P < 0.01$) than for *T. erectus* ($K_D = 8.47$, $N = 15$, $P < 0.05$) (Figure 2.7 and Table 2.17).

Cumulative survival of seed in both burial boxes and bags in time for *T. insignis* and *T. erectus* do not follow the same distribution pattern (Boxes: $K_D = 14.48$, $N = 25$, Bags: $K_D = 21.99$, $N = 15$; $P < 0.01$) (Figure 2.7 and Table 2.17). Cumulative germination of seed in burial boxes in time for *T. insignis* and *T. erectus* do not follow the same distribution pattern ($K_D = 8.01$, $N = 15$, $P < 0.05$) (Figure 2.7 and Table 2.17). Cumulative germination of seed in burial bags in time for *T. insignis* and *T. erectus* do, however, follow the same distribution pattern ($K_D = 4.25$, $N = 25$) (Figure 2.7 and Table 2.17).

Only seed persistence or loss for burial boxes are further reported unless otherwise stated.

2.5.8 SEEDLING DYNAMICS

Seedling and adult densities were estimated from May 1992 to April 1994 at four sampling periods for *T. insignis* and at three sampling periods for *T. erectus*. Seedling emergence in both years occurred mainly from July to August for *T. insignis* and from April to June for *T. erectus*. The major germination period for both the species occurred in autumn and winter after the onset of the annual rains and when the ambient temperatures were declining after the hot summer months (Figure 2.2).

Thamnochortus insignis had a smaller average adult and a greater average seedling density (mean number of individuals per m^2) compared to *T. erectus*, at all sampling times (Table 2.18). In unharvested *T. insignis* vegetation, average (mean ± S.D., n = 100) number of adults and seedlings per m^2 estimated at four sampling periods were 2.26 ± 4.57 and 1.74 ± 2.63, respectively. In unharvested *T. erectus* vegetation, average (mean ± S.D., n = 100) number of adults and seedlings counted at three sampling periods were 0.20 ± 0.74 and 1.87 ± 1.41, respectively. Adult plant density was similar at all sampling times, for both *T. insignis* and *T. erectus* unharvested and harvested vegetation (Table 2.18). *Thamnochortus erectus* seedling density was similar at all sampling times (Table 2.18). The range in seedling density was 2 times for unharvested and 8 times for harvested vegetation. Seedling density was also similar for both harvesting treatments (Table 2.18). *Thamnochortus insignis* seedling density, however, was variable over the four sampling periods (Table 2.18). The range in seedling density was approximately 111 times for unharvested and 133 times for harvested vegetation. Seedling density also differed with harvesting treatment. In unharvested vegetation, average adult density was 1.07 times greater for *T. erectus* than for *T. insignis*, and average seedling density was 11.3 times greater for *T. insignis* than for *T. erectus*. In harvested vegetation, average adult density was 1.45 times and average seedling density was 102 times greater for *T. insignis* than for *T. erectus*. The average density of *T. insignis* adults and seedlings were 1.45 and 1.81 times greater for harvested vegetation compared to unharvested vegetation. The average density of *T. erectus* adults and seedlings was, however, 1.07 and 5 times less for harvested vegetation compared to unharvested vegetation.

Thamnochortus insignis average seedling to parent ratios for all the sampling times was 1.87 for unharvested and 3.18 for harvested vegetation. *Thamnochortus erectus* average seedling to parent ratios for all the sampling times was 0.12 for unharvested and 0.02 for harvested vegetation. *Thamnochortus insignis* had a greater average seedling to parent ratio for all the sampling periods than *T. erectus* for both unharvested (16.26 times) and

harvested (138.17 times) vegetation. Seedling to parent ratios were highly variable between sampling times for *T. insignis*, ranging from 0.02 to 4.23 (222.63 times difference) in unharvested vegetation and from 0.02 to 5.92 (311.58 times difference) in harvested vegetation (Figure 2.8). Seedling to parent ratios were not variable between sampling times for *T. erectus*, ranging from 0.05 to 0.17 (3.09 times difference) in unharvested vegetation and from 0.01 to 0.05 (10.2 times difference) in harvested vegetation (Figure 2.8). For *T. insignis*, the average seedling to parent ratio was 2.7 times greater in harvested than in unharvested vegetation. For *T. erectus*, the average seedling to parent ratio was 5 times greater in unharvested than in harvested vegetation.

Seedlings were not distributed evenly among the different age categories for both species (Table 2.19 and Figure 2.9). The majority of seedlings of both species were less than two years old, with progressively fewer seedlings in the older age categories. The trend was similar at all sampling times, for both harvested and unharvested vegetation (Table 2.19 and Figure 2.9). These results indicate that few seedlings survive to become adult plants and this is especially evident for *T. insignis*. Seedling density in the various age categories varied between harvested and unharvested vegetation, for both species (Table 2.19 and Figure 2.9). The average percentage seedlings in the less than one year age category was 1.10 (*T. insignis*) and 1.08 (*T. erectus*) times less for harvested vegetation compared to unharvested vegetation. The average percentage *T. insignis* seedlings in the one year age category was 1.96 times greater for harvested vegetation compared to unharvested vegetation. *Thamnochortus erectus* had an average of 0% seedlings in this category. The average percentage seedlings in the two year age category was 3.09 (*T. insignis*) and 3.79 (*T. erectus*) times greater for harvested vegetation compared to unharvested vegetation. The average percentage seedlings in the greater than two year age category was 2.37 (*T. insignis*) times less and 2.87 (*T. erectus*) times greater for harvested compared to unharvested vegetation.

Seedling distributions for both species were distinctly patchy and varied widely among microhabitats (Table 2.20 and Figure 2.10). The majority of seedlings of both species were found in "open" microhabitats, with fewer seedlings being found under fynbos vegetation and very few seedlings being found under discarded harvested thatch. The trend was similar at all three sampling periods, for both *T. insignis* and *T. erectus* harvested and unharvested vegetation (Table 2.20 and Figure 2.10). Similar seedling microhabitat preferences were evident in harvested vegetation, although a smaller percentage of seedlings were found under fynbos vegetation (Table 2.20 and Figure 2.10). This may be a direct result of the increase in the frequency of "open" and decrease in the frequency of under fynbos vegetation microhabitat categories, in harvested vegetation.

Thamnochortus insignis adults (average variance to mean ratio for four sampling periods = 4.59, n = 100) and seedlings (average variance to mean ratio for four sampling periods = 6.02, n = 100) were observed to be more clumped than adults (average variance to mean ratio for four sampling periods = 1.07, n = 100) and seedlings (average variance to mean ratio for four sampling periods = 2.91, n = 100) of *T. erectus*, at the 1 X 1 m quadrat scale (i.e. spatial scale) (Table 2.21). Clumping of *T. insignis* individuals over the four sampling periods was highly variable and variance to mean ratios ranged from 1.94 to 9.79 (adults) and 0.26 to 19.15 (seedlings). The degree of clumping of *T. erectus* individuals over the three sampling periods were similar and variance to mean ratios ranged from 0.69 to 1.42 (adults) and 2.36 and 3.58 (seedlings). There was no definite trends in distribution patterns between harvested and unharvested vegetation. *Thamnochortus insignis* individuals were 1.99 (adults) and 1.87 (seedlings) times less clumped in harvested vegetation compared to unharvested vegetation. *Thamnochortus erectus* adults were 1.15 times more clumped and seedlings were 1.56 times less clumped in harvested vegetation compared to unharvested vegetation. In unharvested vegetation, there were no *T. insignis* dead adults and *T. erectus* dead adults were evenly distributed (average variance to mean ratio for three sampling periods = 0.98, n = 100). In

harvested vegetation, *T. insignis* dead adults (average variance to mean ratio for four sampling periods = 3.04, n = 100) were observed to be more clumped than dead adults of *T. erectus* (average variance to mean ratio for three sampling periods = 1.33, n = 100). *Thamnochortus insignis* dead seedlings were highly clumped in both unharvested (variance to mean ratio for one sampling period = 8.10, n = 100) and harvested (variance to mean ratio for one sampling period = 4.09, n = 100) vegetation.

Temporal heterogeneity of adults and seedlings was high (as indicated by variance to mean ratios > 1) for both species (Table 2.22). In unharvested vegetation, *T. insignis* adults (variance to mean ratio = 23.22, n = 4) and seedlings (variance to mean ratio = 226.25, n = 4) were observed to be more clumped in time than adults (variance to mean ratio = 8.10, n = 3) and seedlings (variance to mean ratio = 2.25, n = 3) of *T. erectus*. The especially high variance to mean ratios for *T. insignis* seedlings suggests that a definite recruitment period exist. The same species trends were evident in harvested as in unharvested vegetation (Table 2.22). The degree of *T. insignis* clumping was 2.37 (adults) and 2.69 (seedlings) times greater for harvested vegetation compared to unharvested vegetation. The degree of *T. erectus* clumping was 2.71 times less for adults and 1.74 times greater for seedlings for harvested vegetation compared to unharvested vegetation. Dead *T. insignis* (variance to mean ratio = 10.16, n = 4) adults were temporally clumped in harvested vegetation, indicating that there were not a constant number of dead adults over time. There were no *T. insignis* dead adults in unharvested vegetation. Dead *T. erectus* adults were temporally clumped in harvested vegetation (variance to mean ratio = 1.75, n = 4) and unharvested vegetation (variance to mean ratio = 2.71, n = 4), although the degree of clumping was less than for harvested *T. insignis* adults. This indicates that there was a constant number of *T. erectus* dead adults over time. Many more dead *T. insignis* seedlings were observed in April 1994 compared to any other sampling time, indicating that summer moisture stress may cause seedling mortality in the species. No dead seedlings were observed for *T. erectus*.

The effects of microhabitat, harvesting treatment and sampling period were estimated for *T. insignis* and *T. erectus* data separately using a generalised linear model with a Poisson error distribution and a log link function. A scale factor of 589.3 was used for the *T. insignis* model, indicating considerable over-dispersion, possibly due to the clumping of seedlings. The model, which included microhabitat effect only (Pearsons Chi-squared for the model = 3.28; d.f. = 15; $P > 0.99$), and no harvesting treatment or sampling period effect. The final model explained 67% of the variation in the data (Section 2.9). Using the parameter estimates generated by GLIM, the expected average total number of seedlings that would be found in 100 1 X 1 m quadrats in three microhabitats (i.e. "open", under vegetation and under thatch) was calculated (Section 2.9). The results indicate a microhabitat decrease of 94% in the total numbers of seedlings collected from quadrats placed in under vegetation compared to "open" microhabitats, and a decrease of 99% in the total numbers of seedlings collected from quadrats placed in under thatch compared to "open" microhabitats. For the *T. erectus* model there was significant microhabitat, harvesting and sampling period effects, with no interactions. The final model explained 94% of the variation in the data (Pearsons Chi-squared for the model = 4.94; d.f. = 7; $0.50 > P < 0.75$) (Section 2.9). Using the parameter estimates generated by GLIM, the expected average total number of seedlings that would be found in 100 1 X 1 m quadrats in three microhabitats (i.e. "open", under vegetation and under thatch), in two harvesting treatments (i.e. harvested and unharvested) and at three sampling periods (i.e. August 1993, November 1993 and April 1994) was calculated (Section 2.9). The results indicate a microhabitat decrease of 93% in the total numbers of seedlings collected from quadrats placed in under vegetation compared to "open" microhabitats, and a decrease of 99% in the total numbers of seedlings collected from quadrats placed in under thatch compared to "open" microhabitats. This finding held for all sampling periods and both harvesting treatments. The results reflect an increase of 289% in the total numbers of seedlings collected from quadrats in unharvested vegetation compared to harvested vegetation. This finding held for all microhabitats

and all sampling periods. The results indicate a sampling period increase of 138% in the total numbers of seedlings collected from quadrats in November 1993 compared to August 1993, and no increase in the total numbers of seedlings collected from quadrats in April 1994 compared to August 1993. This finding held for all microhabitats and both harvesting treatments.

2.5.9. SEED BUDGET

T. insignis had greater numbers of plants or propagules than *T. erectus* at all life cycle stages examined for both harvested and unharvested vegetation, except for unharvested adult plants where numbers were similar (Table 2.23). Adult plant numbers of the two species differed in harvested vegetation by approximately 2 times (Table 2.23). Seed production and soil seed bank sizes of the two species differed by approximately 1.40 times for unharvested and 3.70 times for harvested populations. *Thamnochortus insignis*, however, produced about 8 times more seedlings than *T. erectus* (August 1993 and November 1993 were the only comparable sampling periods). There were generally large differences between predicted and actual seed losses for both species, at all three stages of the life cycle examined in unharvested vegetation (Table 2.24). Differences were small for harvested populations of both species (Table 2.25). Both predicted and actual seed loss estimates, for both species, were greater for harvested than for unharvested populations. The life cycle stage at which both species lost most seed was between seed dispersal and incorporation into the soil seed bank (Table 2.24). During this period approximately 84% (*T. insignis*) and 79% (*T. erectus*) of plump seeds produced annually in unharvested vegetation were lost. In *T. insignis*, the production of over 12000 plump seeds per m^2 on average was only to boost seed bank levels by approximately 2000 plump seeds per m^2. In *T. erectus*, the production of over 9000 plump seeds per m^2 on average was only to boost seed bank levels by approximately 1000 plump seeds per m^2. Predicted seed losses were approximately 78% less than actual seed losses during this stage for both species (Table 2.24). In harvested populations of both species, far fewer

plump seed were produced than were counted in the seed bank in harvested vegetation, suggesting that near to 100% of plump seeds produced annually were lost during this period. Predicted seed losses were approximately 9% less than actual seed losses for *T. insignis* and equal to actual seed losses for *T. erectus* during this stage (Table 2.25). During the period from incorporation into the seed bank to twelve months later, for unharvested populations, approximately 12% (*T. insignis*) and 25% (*T. erectus*) of plump seeds were lost. Predicted *T. insignis* seed losses ranged between 21% (burial boxes) and 41% (burial bags) greater than actual seed losses during this stage (Table 2.24). Predicted *T. erectus* seed losses ranged between 17% (burial boxes) and 22% (burial bags) less than actual seed losses during this stage (Table 2.24). No actual seed loss estimate could be made for this time period for harvested populations, as estimates of seed bank densities were not conducted in 1994. Predicted seed losses in the seed bank (excluding losses due to deep burial) for harvested populations, for this time period, were also based on results obtained from the burial box and bag experiment. The assumption is made that rates of seed loss from the seed bank would be similar for unharvested and harvested vegetation. During the period from seed production to storage of seed in the seed bank for twelve months (i.e. the two stages combined), in unharvested vegetation, approximately 93% (*T. insignis*) and 86% (*T. erectus*) of plump seeds were lost. Predicted *T. insignis* seed losses were approximately 40% (burial boxes) and 59% (burial bags) less than actual seed losses during this stage (Table 2.24). Predicted *T. erectus* seed losses were approximately 64% (burial boxes) and 59% (burial bags) less than actual seed losses during this stage (Table 2.24). Predicted seed losses for harvested populations of both species, during this time period, were approximately 100% of annual plump seed production.

Table 2.1. Characteristics of the study species, *Thamnochortus insignis* Masters and *Thamnochortus erectus* (Thunb.) Masters, Restionaceae.

[a] Bond and Goldblatt 1984.

[b] This study.

Characteristic	Species	
	T. insignis	T. erectus
Distribution	Gouritz River mouth to west of Cape Agulhas	From Darling (near Malmesbury) to Knysna
Habitat	Coastal forelands, on young poorly developed sands (0.25-<1m) derived from Bredasdorp Formation limestone	Coastal forelands, on older, better developed sands
Plant height (m)	< 2.5 m	< 1.5 m
Pollination syndrome	Wind	Wind
Dispersal syndrome	Wind	Wind
Flowering	October to March (summer)	August to November (spring)
Pollination	February (summer)	August to September (spring)
Seed dispersal	April to July (autumn to winter)	August to September (winter to spring)
Seed germination	July to August (winter)	April to June (autumn to winter)
Vegetative growth	June to September (winter to spring)	April to May (autumn)
Harvesting	May to August (winter)	December to April (summer to autumn)
Post-fire response	Non-sprouter	Sprouter

Figure 2.1. Map of the location of the study sites, Zoetendalsvallei and Zeekoeivlei, Bredasdorp.

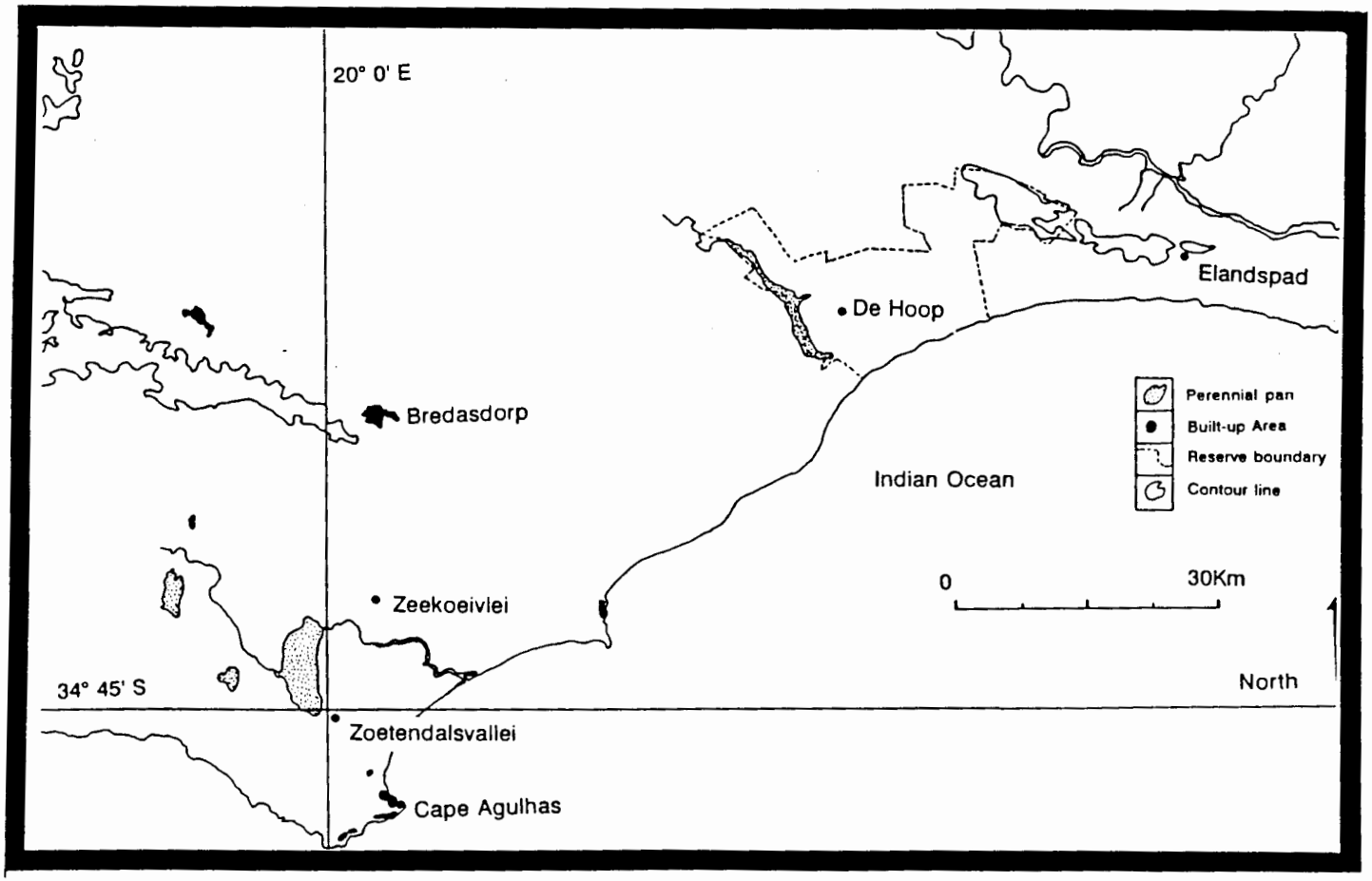


Table 2.2. Physiography, climate and flora of the study sites, Zoetendalsvallei and Zeekoeivlei, Bredasdorp.

	Study site	
	T. insignis	T. erectus
Physiography		
Soils [a]	Unconsolidated, structure-less colluvial sands of mixed origin	Unconsolidated, structure-less colluvial sands of mixed origin
Depth	0.25 - > 0.9 m	0.20 - > 0.9 m
Age	Recent	Older
Texture	Fine - medium	Fine
Colour	Grey	Grey - brown
pH [b]	5.59 + 0.26	5.12 + 0.68
Bedrock	Bredasdorp limestone	Table Mountain sandstone
Climate		
General	Mediterranean type Mild, frost-free	Mediterranean type Mild, frost-free
Mean annual rainfall [c]	460 mm 65 % in winter (May - Oct)	460 mm 65 % in winter (May - Oct)
Mean annual temperature [d]	17.2 C	17.2°C
Mean monthly temperature - Maximum [e]	24°C (January)	24°C (January)
- Minimum [e]	15°C (July)	15°C (July)
Wind speed (mean daily winds) [f]	Windy; 300 km per day	Windy; 300 km per day
Wind direction [f]	Easterly	Easterly
Flora [g]		
Fynbos type	Dry restiod fynbos	Dry restiod fynbos with thicket patches
Years since last fire	11 years [h]	> 15 years [i]
Total projected foliage cover	Ca. 80 %	Ca. 80 %
Dominants (% projected foliage cover)	T. insignis (53 %)	T. erectus (40 %)
Life forms		
Ericoid shrubs	Common (28 %)	Rare (< 1 %)
Proteoid shrubs	Rare (< 1 %)	Absent (0 %)
Large-leaved (non-proteoid) shrubs	Common (3 %)	Very common (39 %)
Grasses	Rare (< 1 %)	Common (17 %)
Graminoids (other than study species)	Rare (< 1 %)	Rare (< 1 %)
Forbs	Rare (< 1 %)	Rare (< 1 %)
Geophytes	Rare (< 1 %)	Rare (< 1 %)
Succulents	Rare (< 1 %)	Rare (< 1 %)
Annuals	Rare (< 1 %)	Rare (< 1 %)
Alien species	Absent (0 %)	Absent (0 %)
Species richness	Moderate-low (38 species)	Moderate-low (35 species)

[a] Thwaites and Cowling 1988.

[b] This study - Mean ± standard deviation (n = 5).

[c] Department of Environmental Affairs, unpublished data (1894 - 1993).

[d] Department of Environmental Affairs, unpublished data (1961 - 1993).

[e] Department of Environmental Affairs, unpublished data (1992 - 1993).

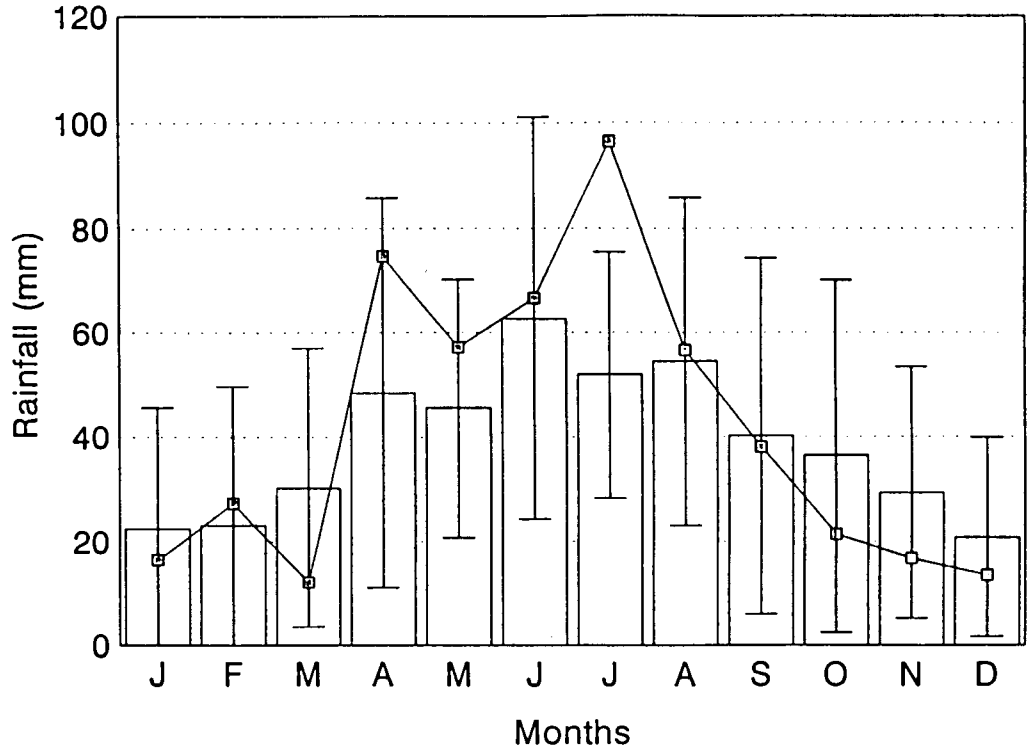
[f] Deacon *et al.* 1992.

[g] This study, using the same methods as Cowling *et al.* 1988.

[h] M. van Breda, personal communication.

[i] P.K. Albertyn, personal communication.

A)



B)

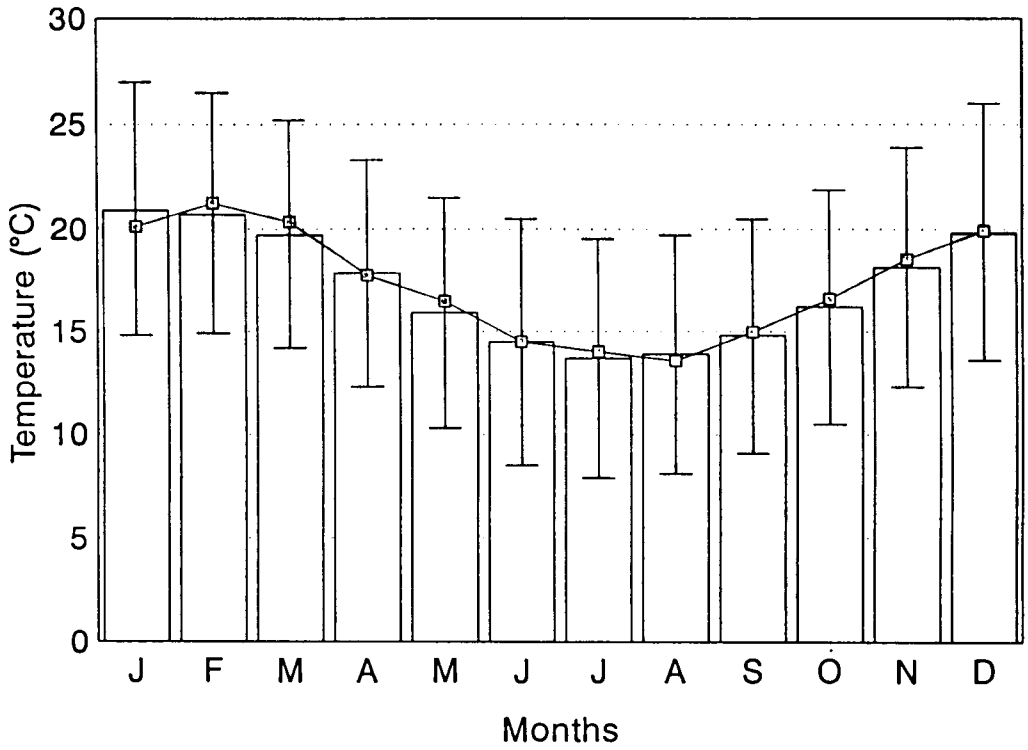


Figure 2.2. Climate diagram for the study sites, Zoetendalsvallei and Zeekoeivlei. Data are from the Cape Agulhas meteorological station (Weather Bureau).

A) Mean monthly rainfall (1894 to 1990) and for study period (from 1990 to 1993) at Cape Agulhas. S.D. are displayed.

B) Mean monthly temperature in degrees Celsius (°C) (from 1961 to 1990) and for the study period (from 1990 to 1993) at Cape Agulhas.
S.D. are displayed.

Table 2.3. Variation within and between *T. insignis* and *T. erectus* seed size characteristics. Data are average seed mass (n = 200 plump seeds per treatment) and seed dimensions (long axis length, short axis length and thickness) (n = 50 plump seeds per treatment) (mean ± standard deviation). Two sample t-tests were used to test within species significance. * * = P < 0.01, * * * = P < 0.001, N.S. = non-significant.

Characteristic	Species									
	T. insignis					T. erectus				
	Year									
	1992		1993			1992		1993		
	Mean	S.D.	Mean	S.D.	Significance within species	Mean	S.D.	Mean	S.D.	Significance within species
Seed mass (mg)	0.899	0.306	1.135	0.338	* * *	1.627	0.579	1.465	0.531	* *
Long axis (mm)	3.327	0.217	3.423	0.305	N.S.	3.655	0.312	3.494	0.238	* *
Short axis (mm)	2.631	0.229	2.560	0.245	N.S.	2.831	0.342	2.720	0.256	N.S.
Thickness (mm)	0.780	0.084	0.872	0.083	* * *	0.977	0.162	0.967	0.085	N.S.

Table 2.4. Estimates of *T. insignis* and *T. erectus* adult plant density. Data are total numbers of adult plants in five 10 X 10 m plots (i.e. 500 m^2) and average (mean ± standard deviation) adult plant density (number of individuals per m^2). Proportions (%) of individuals with respect to the total number of individuals recorded in each category are displayed (n = 5 plots per treatment). Data were collected over two years (1992 and 1993) and in both Area 1 and 2 at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). "Other" refers to all non-reproductive adult plants.

Area	Species															
	T. insignis								T. erectus							
	Year															
	1992				1993				1992				1993			
	Total	%	Mean	S.D.	Total	%	Mean	S.D.	Total	%	Mean	S.D.	Total	%	Mean	S.D.
Area 1																
'Sex' categories:																
Male	513	46.85	1.03	0.36	159	18.34	0.32	0.15	189	40.13	0.39	0.15	51	11.97	0.10	0.03
Female	582	53.15	1.16	0.44	228	26.30	0.46	0.27	246	52.23	0.49	0.13	160	37.56	0.32	0.05
Other	0	0.00	0.00	0.00	480	55.36	0.96	0.51	36	7.64	0.07	0.05	215	50.47	0.43	0.11
Total	1095		2.19	0.79	867		1.73	0.59	471		0.94	0.26	426		0.85	0.13
'Sex' categories (reproductive individuals only):																
Male	513	46.85	1.03	0.36	159	41.09	0.32	0.15	189	43.45	0.39	0.15	51	24.17	0.10	0.03
Female	582	53.15	1.16	0.44	228	58.91	0.46	0.27	246	56.55	0.49	0.13	160	75.83	0.32	0.05
Total	1095		2.19	0.79	387		0.78	0.42	435		0.88	0.28	211		0.42	0.08
Mortality categories:																
Living	1095	100.00	2.19	0.79	867	95.70	1.73	0.59	471	98.95	0.94	0.26	426	98.61	0.85	0.13
Dead	0	0.00	0	0.00	39	4.30	0.08	0.08	5	1.05	0.01	0.01	6	1.39	0.01	0.01
Total	1095		2.19	0.79	906		1.81	0.59	476		0.95	0.95	432		0.86	0.13
Area 2																
'Sex' categories:																
Male	268	44.52	0.54	0.22	255	45.05	0.51	0.26	204	37.02	0.41	0.07	259	38.26	0.52	0.20
Female	334	55.48	0.67	0.33	309	54.60	0.62	0.32	313	56.81	0.63	0.18	400	59.08	0.80	0.44
Other	0	0.00	0.00	0.00	2	0.35	0.004	0.01	34	6.17	0.07	0.04	18	2.66	0.04	0.01
Total	602		1.20	0.55	566		1.13	0.56	551		1.10	0.27	667		1.35	0.63
'Sex' categories (reproductive individuals only):																
Male	268	44.52	0.54	0.22	255	45.21	0.51	0.26	204	39.46	0.41	0.07	259	39.30	0.52	0.20
Female	334	55.48	0.67	0.33	309	54.79	0.62	0.32	313	60.54	0.63	0.18	400	60.70	0.80	0.44
Total	602		1.21	0.55	564		1.13	0.58	517		1.04	0.25	659		1.32	0.64
Mortality categories:																
Living	602	100.00	1.2	0.55	566	100.00	1.13	0.56	551	99.64	1.1	0.27	667	99.71	1.35	0.63
Dead	0	0.00	0.00	0.00	0	0.00	0.00	0.00	2	0.36	0.004	0.01	2	0.29	0.004	0.01
Total	602		1.2	0.55	566		1.13	0.56	553		1.11	0.28	679		1.36	0.63

Table 2.5. Comparisons between observed (obs.) adult plant frequencies (totalled over five 10 X 10 m plots, see Table 2.4) and expected (exp.) adult plant frequencies (calculated from a frequency ratio of 1 male : 1 female plants) for *T. insignis* and *T. erectus*, at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). Chi-squared goodness of fit tests were used on the data. * = P < 0.05, * * = P < 0.01, * * * = P < 0.001, N.S. = non-significant.

Sex' category	Area 1								Area 2							
	Species								Species							
	T. insignis				T. erectus				T. insignis				T. erectus			
	Year								Year							
	1992		1993		1992		1993		1992		1993		1992		1992	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Male	513	547.5	159	193.5	189	217.5	51	105.5	268	301.0	255	282.0	204	258.5	259	329.5
Female	582	547.5	228	193.5	246	217.5	160	105.5	334	301.0	309	282.0	313	258.5	400	329.5
N	1095		387		435		211		602		564		517		659	
Chi-squared statistic	4.4		12.3		7.5		56.3		7.2		5.2		23.0		30.2	
D.f.	1		1		1		1		1		1		1		1	
Significance	*		* * *		* *		* * *		* *		*		* * *		* * *	

Table 2.6. Estimates of *T. insignis* and *T. erectus* plant height and tussock diameter. Data are average (mean ± standard deviation) plant height (ground level to the tallest reproductive culm) (m) and tussock diameter (maximum diameter at ground level) (cm) for living plants. Data were collected at the two study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). Two sample t-tests were used to test within species significance. * * * = $P < 0.001$, N.S. = non-significant.

Area	Species									
	T. insignis					T. erectus				
	Year									
	1992		1993			1992		1993		
	Mean	S.D.	Mean	S.D.	Significance within species	Mean	S.D.	Mean	S.D.	Significance within species
Area 1										
Plant height	1.03	0.20	1.01	0.21	N.S.	1.03	0.21	0.88	0.15	* * *
Tussock diameter	8.50	4.33	11.66	6.53	* * *	43.79	19.96	37.79	18.67	* * *
Area 2										
Plant height	1.16	0.20	1.30	0.23	* * *	1.01	0.20	1.06	0.20	* * *
Tussock diameter	11.13	5.40	14.98	7.02	* * *	44.39	19.82	33.26	18.17	* * *

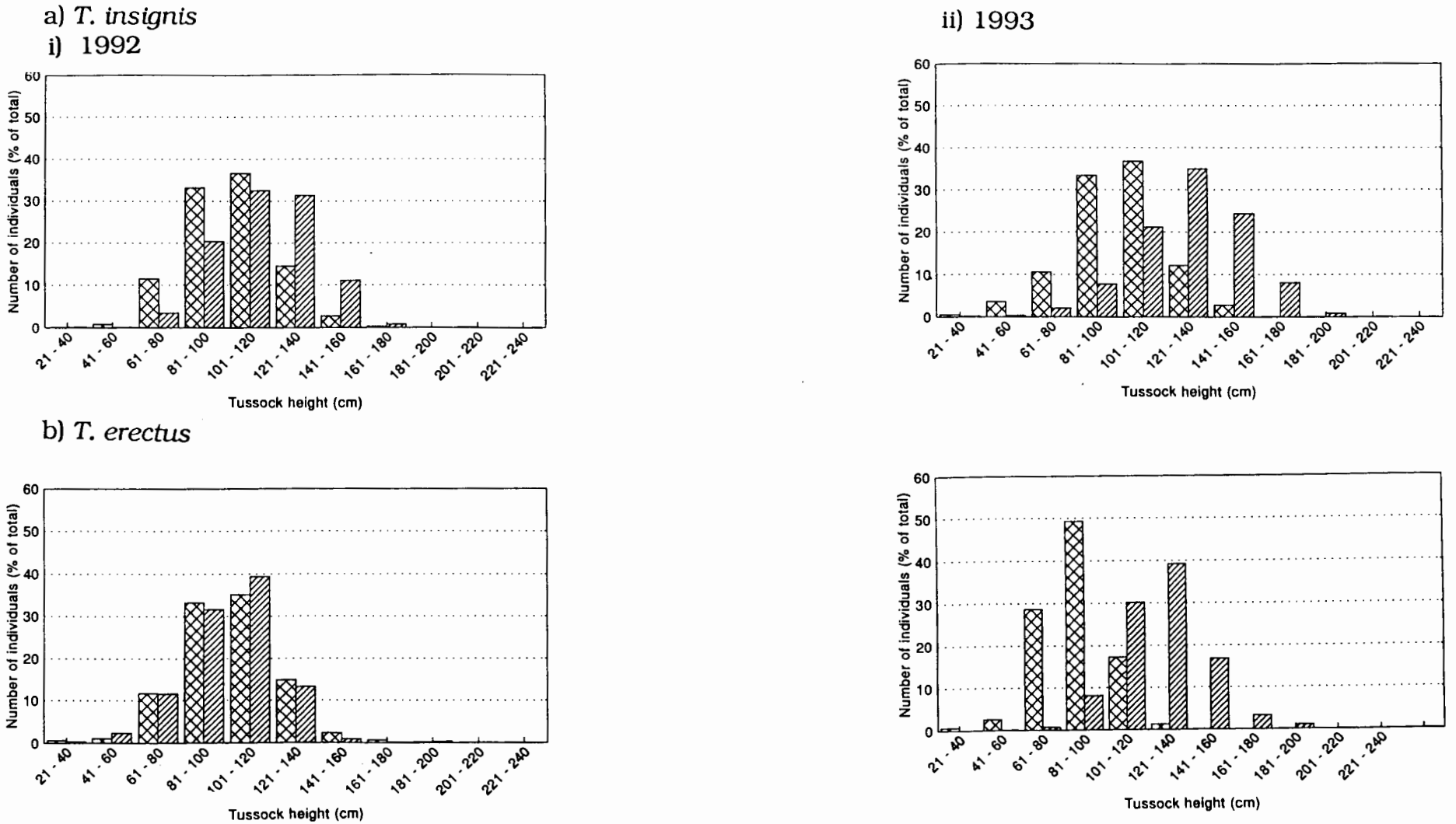


Figure 2.3. Distribution of a) *T. insignis* and b) *T. erectus* reproductive adult plants in plant height (cm) categories. Data are total number of individuals in five 10 X 10 m plots. Proportions (%) of individuals with respect to total numbers of individuals recorded in each category are displayed. Data were collected in both Area 1 ⊠ and Area 2 ▨ in both 1992 and 1993, at the two study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). Area 1 at both study sites was harvested after the 1992 data collection period.

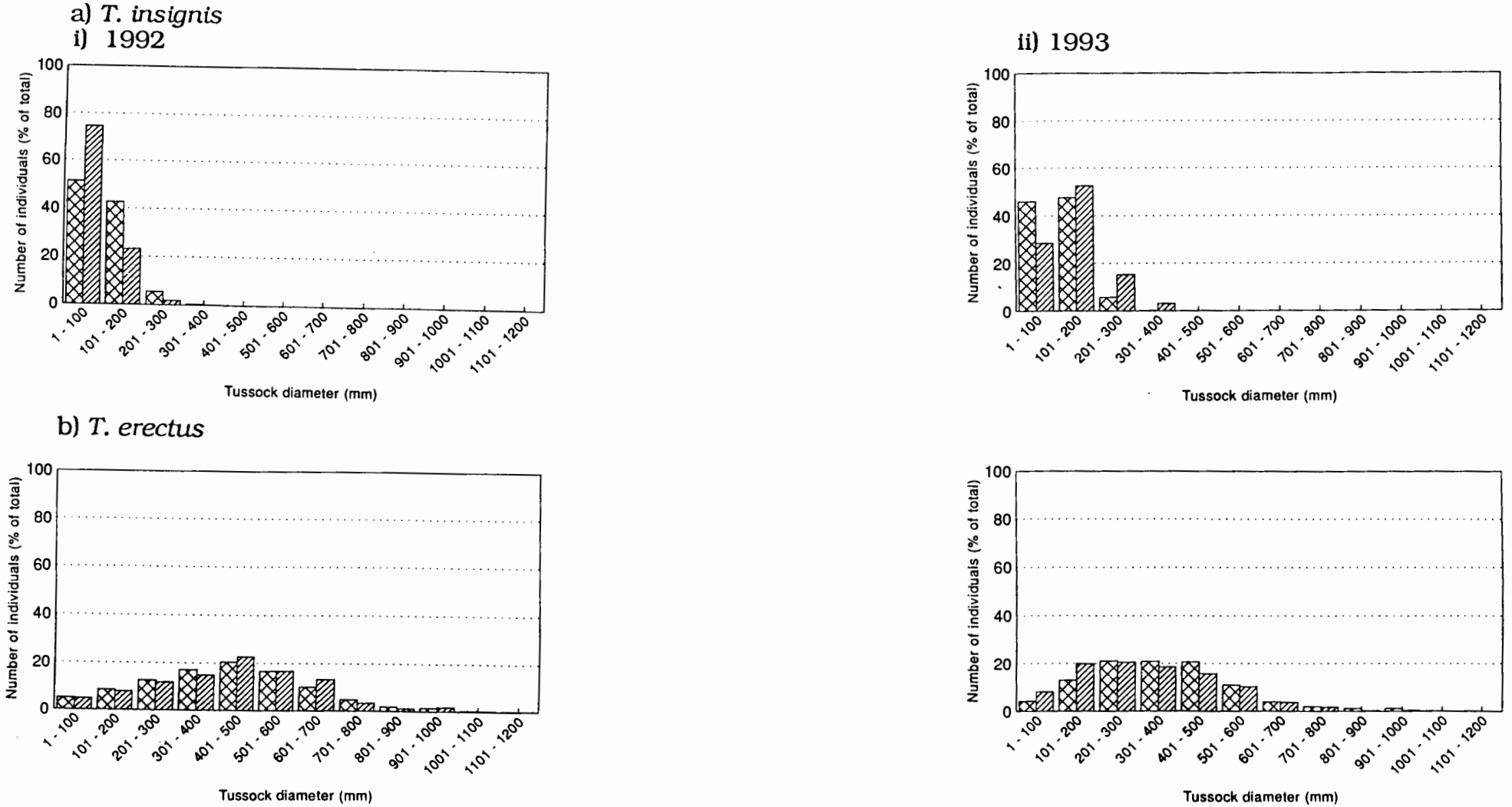
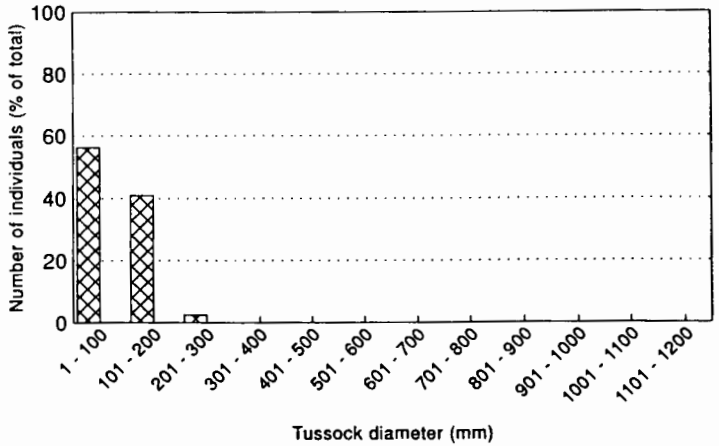


Figure 2.4. Distribution of a) *T. insignis* and b) *T. erectus* live adult plants in plant tussock diameter (mm) categories. Data are total number of individuals in five 10 X 10 m plots. Proportions (%) of individuals with respect to total numbers of individuals recorded in each category are displayed. Data were collected in both Area 1 ⊠ and Area 2 ▨ , in both 1992 and 1993, at the two study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). Area 1 at both study sites was harvested after the 1992 data collection period.

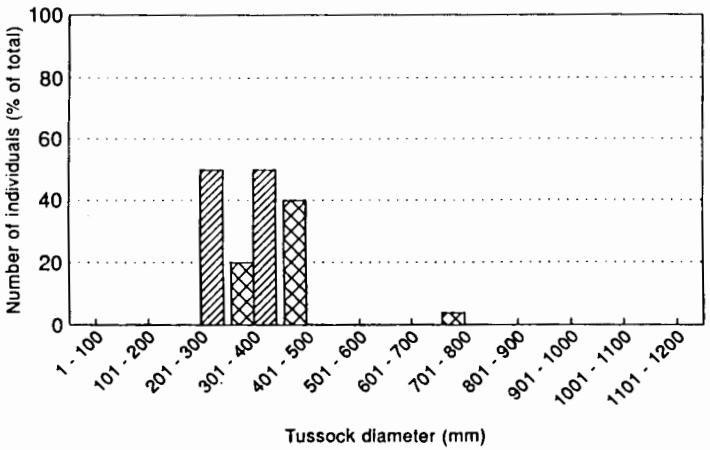
a) *T. insignis*

i) 1992

ii) 1993



b) *T. erectus*



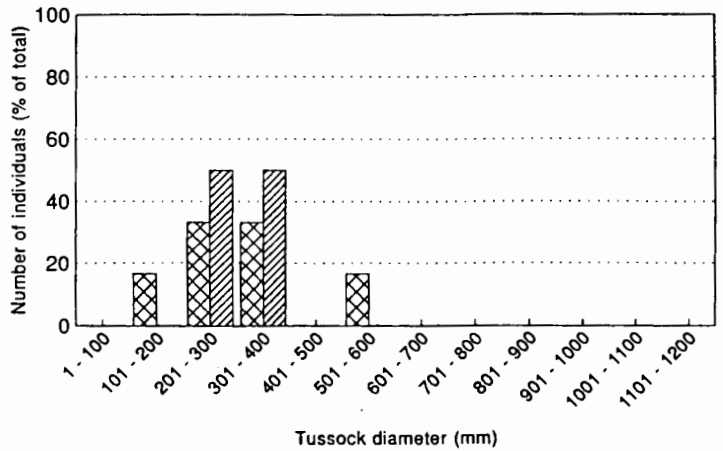


Figure 2.5. Distribution of a) *T. insignis* and b) *T. erectus* dead adult plants in plant tussock diameter (mm) categories. Data are total number of individuals in five 10 X 10 m plots. Proportions (%) of individuals with respect to total numbers of individuals recorded in each category are displayed. Data were collected in both Area 1 'key' and Area 2 'key', in both 1992 and 1993, at the two study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). Area 1 at both study sites was harvested after the 1992 data collection period. There were no *T. insignis* dead adult plants in 1992.

Table 2.7. Estimates of *T. insignis* and *T. erectus* plump, aborted and predated seed. Data are total number of plump (i.e. contains an endosperm), aborted (i.e. not plump - containing no endosperm) and predated seeds in 20 mature female inflorescences, and average number (mean ± standard deviation) of plump (i.e. contains an endosperm), aborted (i.e. not plump - containing no endosperm) and predated seeds per inflorescence (n = 20 culms per treatment). Proportions (%) of seeds with respect to the total number of seeds recorded in each category are displayed. Data were collected for the current year's female inflorescences, over two years (1992 and 1993) and in both Area 1 and 2 at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

Area	Species							
	T. insignis				T. erectus			
	Year							
	1992		1993		1992		1993	
	Total (%)	Mean ± S.D.	Total (%)	Mean ± S.D.	Total (%)	Mean ± S.D.	Total (%)	Mean ± S.D.
Area 1								
Plump seeds	7351 (95.07)	367.55 ± 115.71	2379 (70.85)	118.95 ± 105.51	3065 (94.13)	153.25 ± 86.09	513 (69.32)	25.65 ± 20.58
Aborted seeds	222 (2.87)	11.1 ± 8.43	356 (10.60)	17.8 ± 22.29	157 (4.82)	7.85 ± 10.31	169 (22.84)	8.45 ± 14.30
Predated seeds	159 (2.06)	7.95 ± 5.61	623 (18.55)	31.15 ± 18.35	34 (1.05)	1.7 ± 2.3	58 (7.84)	2.9 ± 5.12
Total	7732	386.6 ± 118.02	3358	167.9 ± 101.93	3256	162.8 ± 86.93	740	37 ± 28.38
Area 2								
Plump seeds	7700 (93.79)	385 ± 194.88	6723 (91.96)	336.15 ± 211.82	2740 (93.07)	137 ± 84.69	3193 (95.97)	159.65 ± 83.28
Aborted seeds	124 (1.51)	6.2 ± 5.62	163 (2.23)	8.15 ± 5.92	191 (6.49)	9.55 ± 16.55	99 (2.98)	4.95 ± 6.67
Predated seeds	386 (4.70)	19.3 ± 15.48	425 (5.81)	21.25 ± 15.34	13 (0.44)	0.65 ± 1.04	35 (1.05)	1.75 ± 2.97
Total	8210	410.5 ± 206.23	7311	365.55 ± 219.29	2944	147.2 ± 93.23	3327	166.35 ± 88.76

Table 2.8. Statistics of *T. insignis* and *T. erectus* reproductive structures and seed production. Data are average values (mean ± standard deviation) for inflorescence length (in mm) (n = 100), number of inflorescences per plant (n = 50), number of spiklets per inflorescence (n = 100), number of plump seeds per inflorescence (n = 100), number of plump seeds per plant, number of inflorescences per m^2, number of plump seeds per m^2, plump seed mass per m^2, total number of seeds per m^2 and total seed mass per m^2 for *T. insignis* and *T. erectus* at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). Data were collected for the current year's female inflorescences, over two years (1992 and 1993) and in both Area 1 and 2.

Area	Species							
	T. insignis				T. erectus			
	Year							
	1992		1993		1992		1993	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Area 1								
Inforescence length (mm)	110.1	37.8	75.6	39.3	80.9	49.8	42.7	26.0
Inflorescences/plant	60	34	6	5	58	36	4	6
Spiklets/inflorescence	11	6	5	2	4	2	2	1
Plump seeds/inflorescence	392	174	103	90	148	79	36	36
Plump seeds/plant	23363	5882	645	422	8641	2818	151	220
Inflorescences/m square	69	15	3	1	29	5	1	< 1
Plump seeds/m square	27194	2588	294	114	4251	366	48	11
Seed mass (g)/m square	24.447	2.326	0.333	0.129	6.916	0.596	0.070	0.016
Total seeds/m square	28604	2722	414	161	4516	389	69	16
Total seed mass (g)/m square	25.715	2.447	0.470	0.183	7.348	0.633	0.101	0.023
Area 2								
Inforescence length (mm)	106.3	40.3	146.8	52.8	69.6	41.3	82.1	42.5
Inflorescences/plant	74	70	45	42	62	42	106	91
Spiklets/inflorescence	10	4	7	2	4	2	3	1
Plump seeds/inflorescence	353	176	288	172	145	102	151	90
Plump seeds/plant	25965	12402	12859	7296	9034	4294	15944	8206
Inflorescences/m square	49	23	28	14	39	8	85	40
Plump seeds/m square	17345	4093	7948	2335	5656	773	12755	3611
Plump seed mass (g)/m square	15.594	3.679	9.021	2.650	9.202	1.258	18.685	5.289
Total seeds/m square	18494	4364	8642	2539	6077	830	13290	3762
Total seed mass (g)/m square	16.626	3.923	9.809	2.882	9.887	1.350	19.470	5.511

Table 2.9. Three-way analysis of variance on the effects of species, year and harvesting treatment on inflorescence length. N.S. = non-significant.

Source of variation	df	F	P*
Species	1	190.18	< 0.001
Year	1	2.78	N.S.
Harvesting treatment	1	64.96	< 0.001
Interactions:			
Species x Year	1	7.14	< 0.01
Species x Harvesting treatment	1	10.99	< 0.01
Year x Harvesting treatment	1	112.28	< 0.001
Species x Year x Harvesting treatment	1	4.24	< 0.05

Table 2.10. Three-way analysis of variance on the effects of species, year and harvesting treatment on number of spiklets per inflorescence. Data were square root transformed, after 0.5 was added (many small data). N.S. = non-significant.

Source of variation	df	F	P*
Species	1	912.61	< 0.001
Year	1	284.36	< 0.001
Harvesting treatment	1	34.88	< 0.001
Interactions:			
Species x Year	1	38.82	< 0.001
Species x Harvesting treatment	1	0.01	N.S.
Year x Harvesting treatment	1	39.16	< 0.001
Species x Year x Harvesting treatment	1	33.07	< 0.001

Table 2.11. Three-way analysis of variance on the effects of species, year and harvesting treatment on number of plump seeds per inflorescence. Data were square root transformed, after 0.5 was added (many small data). N.S. = non-significant.

Source of variation	df	F	P*
Species	1	425.06	< 0.001
Year	1	276.17	< 0.001
Harvesting treatment	1	119.51	< 0.001
Interactions:			
Species x Year	1	28.93	< 0.001
Species x Harvesting treatment	1	0.09	N.S.
Year x Harvesting treatment	1	182.74	< 0.001
Species x Year x Harvesting treatment	1	1.82	N.S.

Table 2.12. Estimates of post-dispersal seed predation of *T. insignis* and *T. erectus*. Data are average numbers of seeds remaining (mean ± standard deviation) in depots of four treatments in the cafeteria experiment. Treatment 1 depots excluded invertebrates; treatment 2 excluded small mammals; treatment 3 was open to both invertebrates and small mammals and treatment 4 was closed to both invertebrates and small mammals. Ten depots for each treatment were checked for damage and seeds counted and missing seeds replaced (total seeds: *T. insignis* 40 and *T. erectus* 30) on three successive sunny days (n = 3). Data were collected at the two study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). Data were collected in the morning (just after sunrise) and evening (just before sunset).

Cafeteria treatment	Area							
	Area 1				Area 2			
	Time of count							
	Morning		Evening		Morning		Evening	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
T.insignis								
Treatment 1	40.10	0.17	39.23	0.78	39.97	0.06	39.63	0.32
Treatment 2	39.77	0.25	38.83	1.76	40.00	0.10	39.67	0.51
Treatment 3	39.70	0.26	38.90	1.28	40.00	0.10	39.80	0.20
Treatment 4	39.97	0.06	39.43	0.55	39.60	0.53	39.77	0.32
T. erectus								
Treatment 1	23.97	4.21	28.83	1.04	25.00	4.16	28.03	1.62
Treatment 2	26.33	5.06	28.50	2.25	25.93	5.23	29.30	0.79
Treatment 3	25.83	5.11	28.63	1.44	25.47	4.07	27.30	2.51
Treatment 4	26.17	4.74	29.27	1.62	26.10	4.26	28.70	1.41

Table 2.13. Seed bank sizes of *T. insignis* and *T. erectus* at two soil depths. Data are total numbers of seeds in 50 paired soil core samples (981.75 cm^2 area of soil/9817.48 cm^3 volume of soil) taken at two soil depths, namely shallow (0 - 10 cm) and deep (10 - 20 cm). Proportions (%) of seeds with respect to the total number of seeds recorded in each category are displayed. Data were collected over two years (1992 and 1993), at two time periods (before and after dispersal) and in both Area 1 and 2 at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

Area	Species							
	T. insignis				T. erectus			
	Year							
	1992		1993		1992		1993	
	Total	%	Total	%	Total	%	Total	%
Area 1								
Before dispersal								
Soil depth								
Shallow	12	63.16	47	94.00	71	95.95	126	96.18
Deep	7	36.84	3	6.00	3	4.05	5	3.82
Total	19		50		74		131	
After dispersal								
Soil depth								
Shallow	188	95.92	209	83.94	166	86.91	71	70.30
Deep	8	4.08	40	16.06	25	13.09	30	29.70
Total	196		249		191		101	
Area 2								
Before dispersal								
Soil depth								
Shallow	18	85.71	89	88.12	39	95.12	196	97.51
Deep	3	14.29	12	11.88	2	4.88	5	2.49
Total	21		101		41		201	
After dispersal								
Soil depth								
Shallow	327	97.03	434	87.85	190	86.36	256	96.60
Deep	10	2.97	60	12.15	30	13.64	9	3.40
Total	337		494		220		265	

Table 2.14. Seed bank sizes of *T. insignis* and *T. erectus* before and after harvesting treatments. Data are total number of seeds recorded in 150 soil core samples (8835.73 cm^2 area of soil/88357.29 cm^3 volume of soil), and average number of seeds per m^2 (mean ± standard deviation) (n = 150 soil core samples per treatment), collected using the physical separation technique. Data were collected over two years (1992 and 1993), at two time periods (before and after dispersal) and in both Area 1 and 2 at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

Area	Species							
	T. insignis				T. erectus			
	Year							
	1992		1993		1992		1993	
	Total	Mean ± S.D.	Total	Mean ± S.D.	Total	Mean ± S.D.	Total	Mean ± S.D.
Area 1								
Before dispersal	44	49.8±112.2	1345	1522.4±1759.4	708	801.4±1386.9	1107	1253.0±1451.6
After dispersal	2243	2538.8±2877.6	1225	1386.5±2161.7	2592	2933.8±4025.8	379	429.0±617.6
Area 2								
Before dispersal	184	208.3±423.8	2702	3058.3±4778.9	284	321.4±549.1	1719	1945.7±4738.2
After dispersal	3075	3480.5±6066.2	3592	4065.6±5986.8	2285	2586.3±4275.4	2186	2474.3±2689.2

Table 2.15. Seed bank sizes of *T. insignis* and *T. erectus* before and after harvesting treatments. Data are total number of seedlings recorded in 10 soil core samples (196.35 cm^2 area of soil/1963.50 cm^3 volume of soil), and average number of seedlings per m^2 (mean ± standard deviation) (n = 10 soil core samples per treatment), collected using the seedling emergence technique. Data were collected over two years (1992 and 1993), at one time period (after dispersal), in both Area 1 and 2, at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

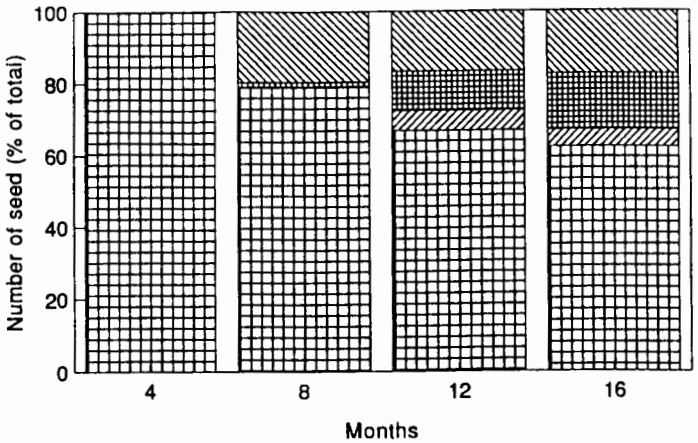
Treatment	Species							
	T. insignis				T. erectus			
	Year							
	1992		1993		1992		1993	
	Total	Mean S.D.	Total	Mean S.D.	Total	Mean S.D.	Total	Mean S.D.
Area 1.								
After dispersal	5	254.7 432.9	2	101.9 322.2	5	254.7 360.2	1	50.9 161.1
Area 2.								
After dispersal	20	1018.8 1074.0	21	1069.8 1280.9	14	713.2 547.6	16	815.1 644.4

Table 2.16. Spatial heterogeneity of *T. insignis* and *T. erectus* seed counts (obtained by the direct count and seedling emergence techniques), as measured by variance to mean ratios. Data were collected over two years (1992 and 1993) and in both Area 1 and 2 at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). Data were collected at two time periods (before and after dispersal) using the physical separation technique and at one time period (after dispersal) using the seedling emergence technique.

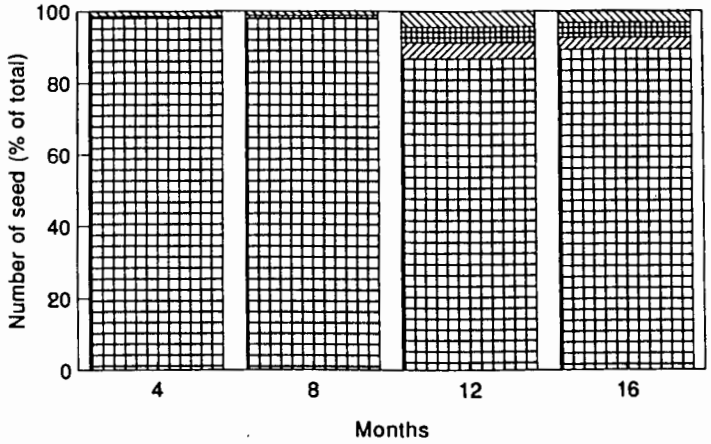
Technique	Species			
	T. insignis		T. erectus	
	Year			
	1992	1993	1992	1993
a) Physical separation technique:				
Area 1				
Before dispersal	1.49	11.98	14.14	14.87
After dispersal	19.21	19.85	32.54	5.22
Area 2				
Before dispersal	5.08	43.98	5.52	30.19
After dispersal	62.27	51.92	41.63	17.21
b) Seedling emergence technique:				
Area 1				
After dispersal	1.44	2.00	1.00	1.00
Area 2				
After dispersal	2.22	3.01	0.83	1.00

a) *T. insignis*

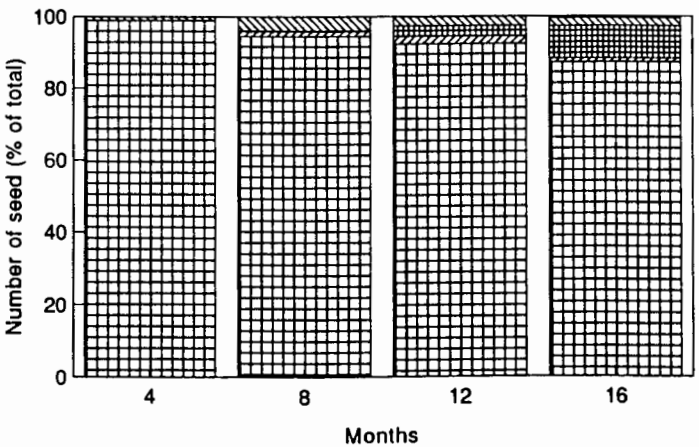
i) Burial boxes



ii) Burial bags



b) *T. erectus*



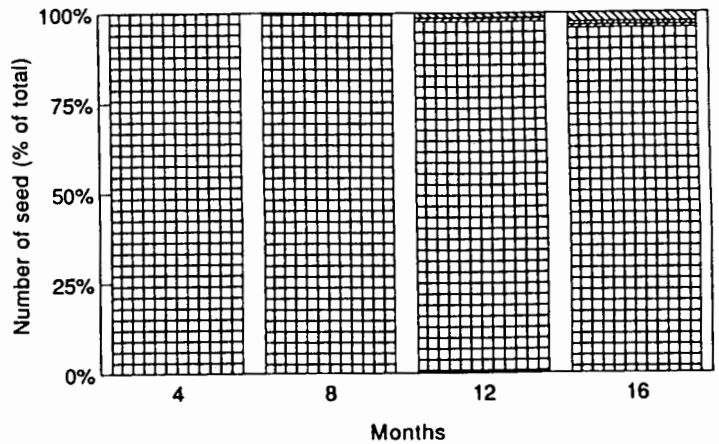


Figure 2.6. Percentage a) *T. insignis* and b) *T. erectus* seed in the plump (i.e. contains endosperm) ⊞ , predated ▨ , germinated (i.e. successful and failed germination) ▦ and "lost" (i.e. decayed and failed early germination) ▧ seed categories after 4, 8, 12 and 16 months of field exposure at the study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). Data are average percentages (mean ± standard deviation) of seeds in each category per burial box or burial bag. A total of 25 seeds were placed in each bag (n = 15 bags per treatment) and a total of 100 seeds were placed in each box (n = 25 boxes per treatment). Seeds were buried at approximately 1 cm below the soil surface.

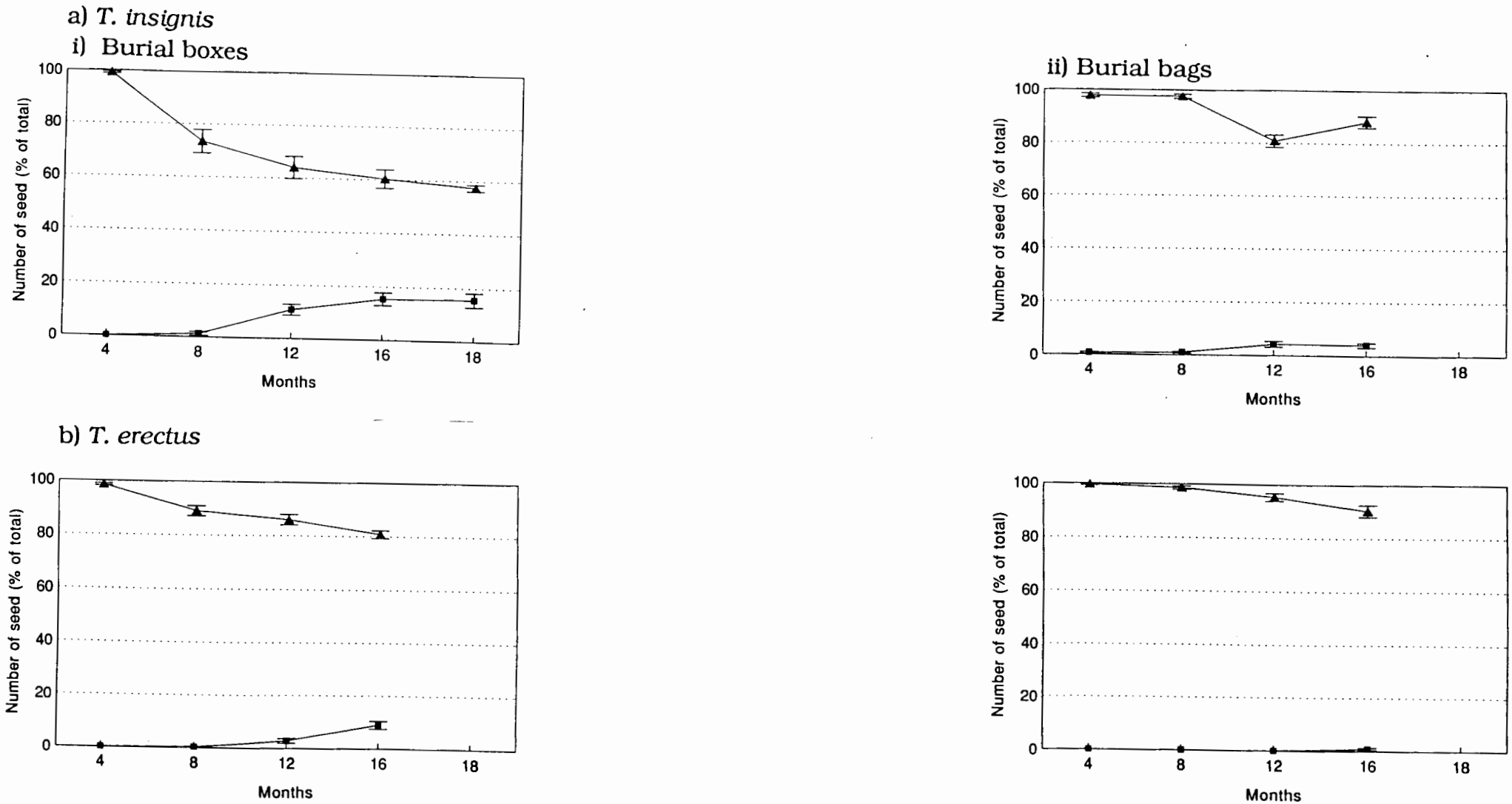


Figure 2.7. Cumulative survival ▲ and germination ▪ of a) *T. insignis* and b) *T. erectus* seeds after 4, 8, 12, 16 and 18 months of field exposure at the study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). Data are average percentages (mean ± standard deviation) of germinated seeds per box or bag. A total of 50 *T. insignis* and 25 *T. erectus* seeds were placed in each bag (n = 15 bags per treatment). A total of 200 *T. insignis* and 100 *T. erectus* seeds were placed in each box (n = 25 boxes per treatment). Seeds were buried at approximately 1 cm below the soil surface. Data for the 18 month sampling period are available for *T. insignis* boxes only.

Table 2.17. Significance of the Kolmogrov-Smirnov two-sample test on the differences in cumulative survival and germination of *T. insignis* and *T. erectus* seeds, over time, in both burial boxes and burial bags (n = 15). A total of 50 *T. insignis* and 25 *T. erectus* seeds were placed in each bag (n = 15 bags per treatment). A total of 200 *T. insignis* and 100 *T. erectus* seeds were placed in each box (n = 25 boxes per treatment). Seeds were buried at approximately 1 cm below the soil surface at the study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). Data were collected at approximately four month intervals for 18 months in 1992 and 1993. * = $P < 0.05$, * * = $P < 0.01$, N.S. = non-significant.

			T. erectus			
			Survival		Germination	
			Burial box	Burial bag	Burial box	Burial bag
T. insignis	Survival	Burial box	* *			
		Burial bag		* *		
	Germination	Burial box			*	
		Burial bag				N.S.

			Burial bag			
			Survival		Germination	
			T. insignis	T. erectus	T. insignis	T. erectus
Burial box	Survival	T. insignis	* *			
		T. erectus		* *		
	Germination	T. insignis			* *	
		T. erectus				*

Table 2.18. Estimated *T. insignis* and *T. erectus* seedling and adult plant densities. Data are total numbers of seedlings and adult plants recorded in 100 1 X 1 m quadrats, and average numbers of seedlings and adult plants (mean ± standard deviation) per m^2 (n = 100 quadrats per treatment). Counts were made in both harvested (i.e. Area 1) and unharvested (i.e. Area 2) vegetation over three years (1992, 1993 and 1994). There were at four (May 1992, August 1993, November 1993 and April 1994) sampling periods for *T. insignis* and three (December 1992, August 1993 and April 1994) sampling periods for *T. erectus*. Data were collected at the two study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

Species	Area							
	Area 1				Area 2			
	Adults		Seedlings		Adults		Seedlings	
	Total	Mean ± S.D.	Total	Mean ± S.D.	Total	Mean ± S.D.	Total	Mean ± S.D.
T. insignis								
Sampling period 1	417	4.24 ± 3.74	8	0.08 ± 0.44	264	2.65 ± 3.16	5	0.05 ± 0.22
Sampling period 2	232	2.36 ± 2.35	34	0.34 ± 0.77	167	1.70 ± 2.20	39	0.39 ± 1.21
Sampling period 3	162	1.68 ± 1.57	523	5.23 ± 6.65	102	1.27 ± 3.53	307	3.07 ± 7.67
Sampling period 4	180	1.83 ± 1.97	1065	10.65 ± 16.44	131	1.35 ± 1.62	554	5.54 ± 9.19
T. erectus								
Sampling period 1	163	1.63 ± 1.06	2	0.02 ± 0.14	144	1.45 ± 1.01	24	0.24 ± 0.82
Sampling period 2	201	2.01 ± 1.96	1	0.01 ± 0.10	221	2.22 ± 1.57	12	0.12 ± 0.66
Sampling period 3	158	1.60 ± 1.33	8	0.08 ± 0.27	187	1.93 ± 1.65	23	0.23 ± 0.74

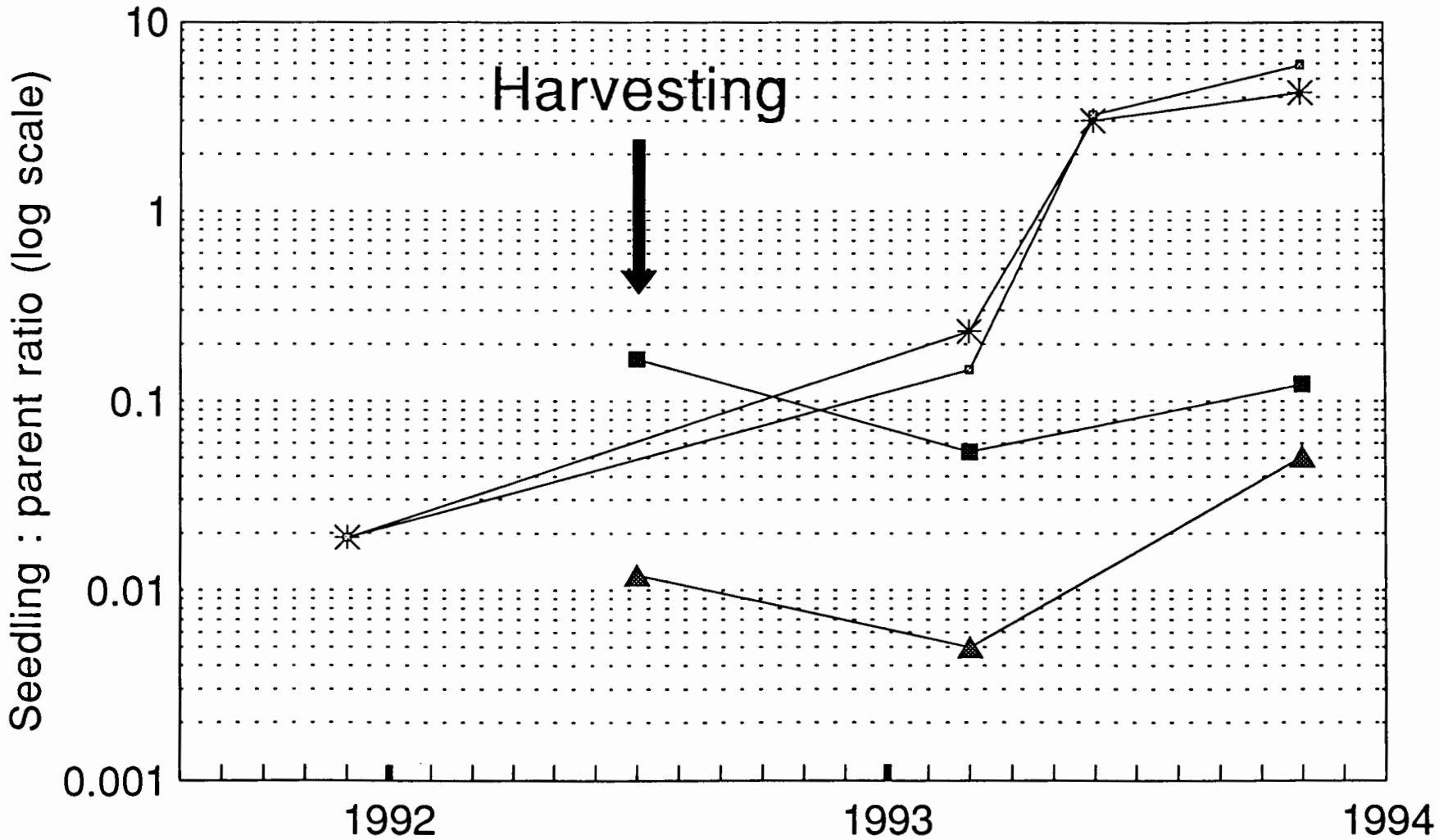


Figure 2.8. Estimated *T. insignis* and *T. erectus* seedling : parent ratios. Data are for all live individuals recorded in 100 1 X 1 m quadrats (i.e. 100 m^2). Counts were made in both harvested (i.e. Area 1) (*T. insignis*: —▫— and *T. erectus*: —▲—) and unharvested (i.e. Area 2) (*T. insignis*: —✳— and *T. erectus*: —■—) vegetation over three years (1992, 1993 and 1994). There were four (May 1992, August 1993, November 1993 and April 1994) sampling periods for *T. insignis* and three (December 1992, August 1993 and April 1994) sampling periods for *T. erectus*. Data were collected at the two study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

Table 2.19. Estimated *T. insignis* and *T. erectus* seedling age structure. Data are total numbers of seedlings in four distinct age categories (< 1 year old, 1 year old, 2 years old and > 2 years old) recorded in 100 1 X 1 m quadrats (i.e. 100 m^2). Proportions (%) of seedlings with respect to the total number of seedlings recorded in each category are displayed. Seedling counts were made in both harvested (i.e. Area 1) and unharvested (i.e. Area 2) vegetation over two years (1993 and 1994). There were three (August 1993, November 1993 and April 1994) sampling periods for *T. insignis* and two (August 1993 and April 1994) sampling periods for *T. erectus*. Data were collected at the two study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

Treatment	Age categories							
	< One year old		One year old		Two years old		> Two years old	
	Total	%	Total	%	Total	%	Total	%
T. insignis								
Harvested								
Sampling period 1	27	79.41	7	20.59	0	0.00	0	0.00
Sampling period 2	457	87.38	50	9.56	11	2.10	5	0.96
Sampling period 3	825	77.47	187	17.56	42	3.94	11	1.03
Unharvested								
Sampling period 1	34	87.18	5	12.82	0	0.00	0	0.00
Sampling period 2	278	90.55	15	4.89	1	0.33	13	4.23
Sampling period 3	505	91.16	37	6.68	9	1.62	3	0.54
T. erectus								
Harvested								
Sampling period 1	0	0.00	0	0.00	1	100.00	0	0.00
Sampling period 2	5	62.50	0	0.00	1	12.50	2	25.00
Unharvested								
Sampling period 1	5	41.67	5	41.67	2	16.66	0	0.00
Sampling period 2	6	26.09	12	52.17	3	13.04	2	8.70

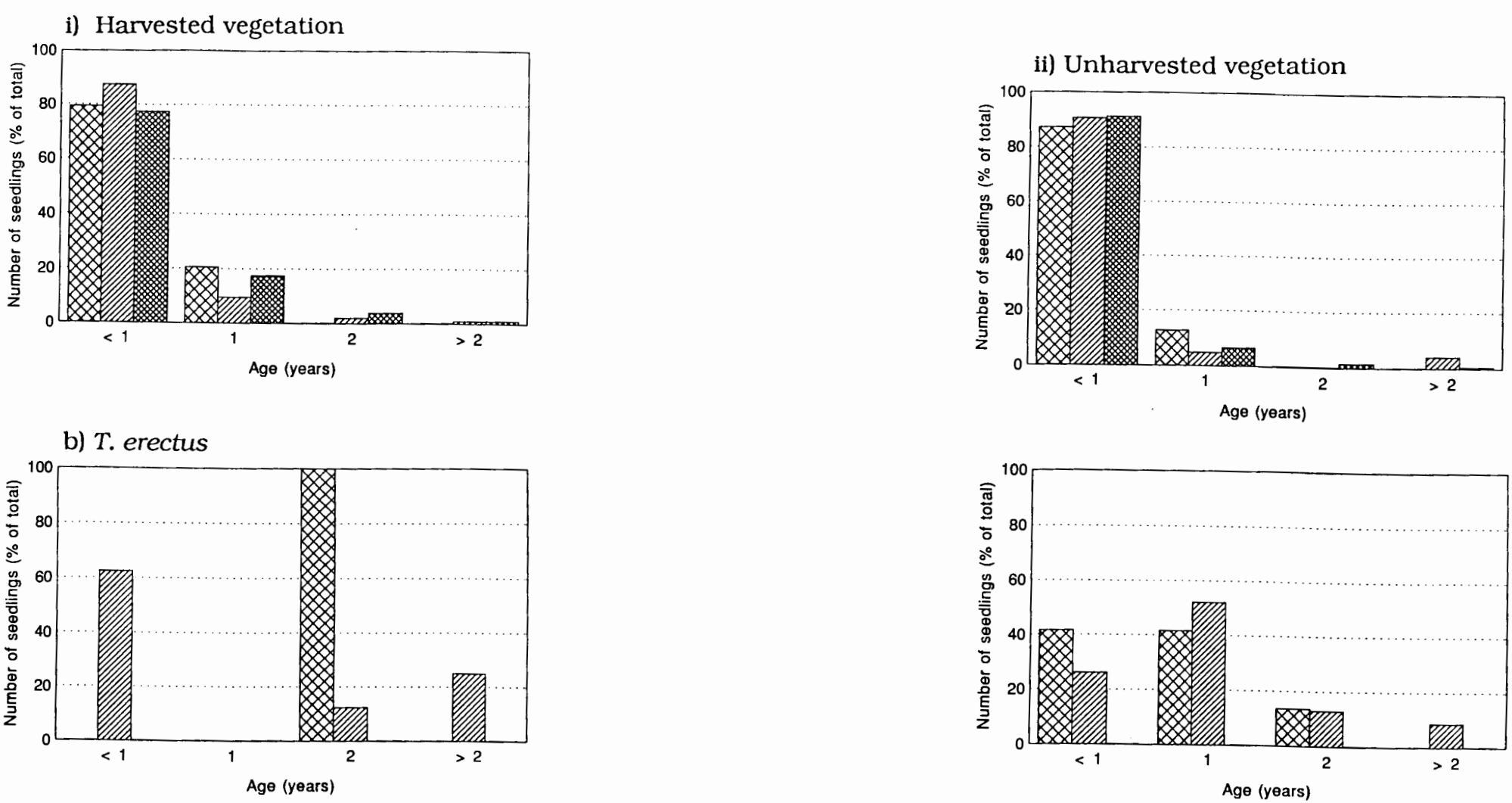


Figure 2.9. Percentage a) *T. insignis* and b) *T. erectus* seedlings in four distinct age categories (< 1 year old, 1 year old, 2 years old and > 2 years old) recorded in 100 1 X 1 m quadrats (i.e. 100 m^2). Seedling counts were made in both harvested (i.e. Area 1) and unharvested (i.e. Area 2) vegetation over two years (1993 and 1994). There were three (August 1993 ⊠ ', November 1993 ▨ and April 1994 ▩ '\ sampling periods for *T. insignis* and two (August 1993 ⊠ and April 1994 ▨) sampling periods for *T. erectus*. Data were collected at the two study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

Table 2.20. Variations in *T. insignis* and *T. erectus* seedling numbers in three distinct microhabitats. Data are total numbers of seedlings recorded in "open" areas, under vegetation and under thatch, in 100 randomly placed 1 X 1 m quadrats (i.e. 100 m^2). Proportions (%) of seedlings with respect to the total number of seedlings recorded in each category are displayed. Seedling counts were made in both harvested (i.e. Area 1) and unharvested (i.e. Area 2) vegetation over two years (1993 and 1994). There were three (August 1993, November 1993 and April 1994) sampling periods for *T. insignis* and two (August 1993 and April 1994) sampling periods for *T. erectus*. Data were collected at the two study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

Treatment	Microhabitat					
	Open area		Under vegetation		Under thatch	
	Total	%	Total	%	Total	%
T. insignis						
Harvested						
Sampling period 1	31	91.18	3	8.82	0	0.00
Sampling period 2	523	100.00	0	0.00	0	0.00
Sampling period 3	1001	93.99	64	6.01	0	0.00
Unharvested						
Sampling period 1	26	66.67	8	20.51	5	12.82
Sampling period 2	307	100.00	0	0.00	0	0.00
Sampling period 3	485	87.55	69	12.45	0	0.00
T. erectus						
Harvested						
Sampling period 1	2	100.00	0	0.00	0	0.00
Sampling period 2	1	100.00	0	0.00	0	0.00
Sampling period 3	8	100.00	0	0.00	0	0.00
Unharvested						
Sampling period 1	24	100.00	0	0.00	0	0.00
Sampling period 2	12	100.00	0	0.00	0	0.00
Sampling period 3	20	86.96	3	13.04	0	0.00

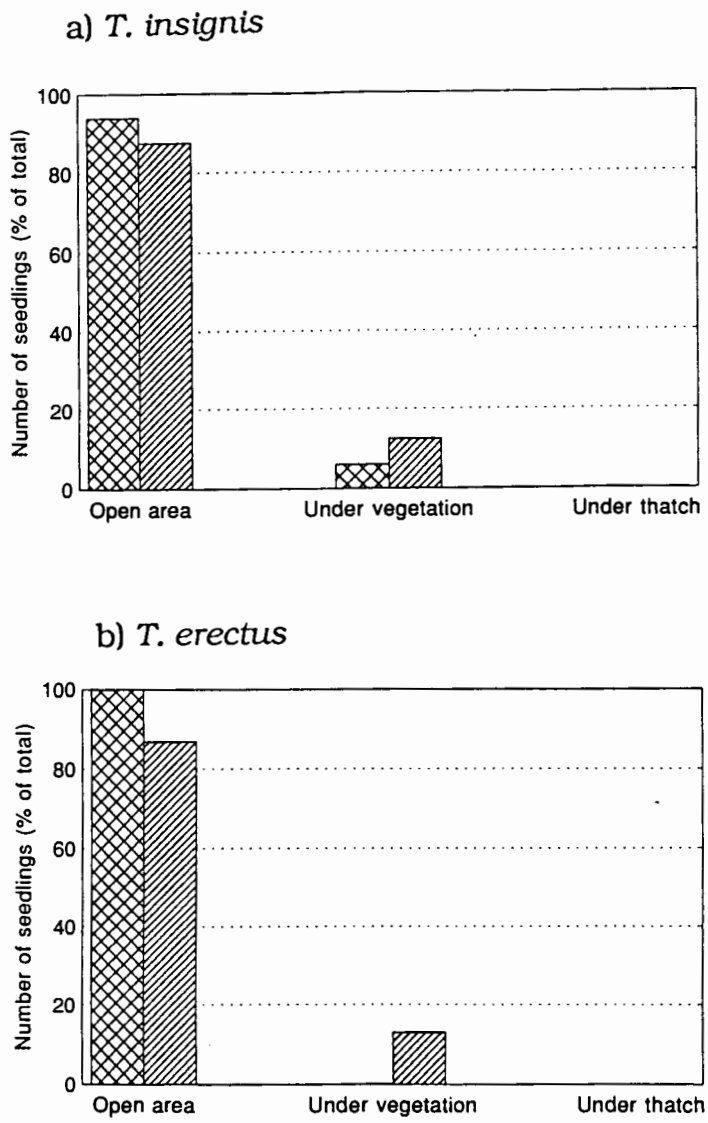


Figure 2.10. Percentage a) *T. insignis* and b) *T. erectus* seedlings in three distinct microhabitats ("open" area, under vegetation and under thatch) recorded in 100 1 X 1 m quadrats (i.e. 100 m^2). Seedling counts were made in both harvested (i.e. Area 1) ⊠ and unharvested (i.e. Area 2) vegetation ▨ over two years (1993 and 1994). There were three (August 1993, November 1993 and April 1994) sampling periods for *T. insignis* and two (August 1993 and April 1994) sampling periods for *T. erectus*. The patterns of seedlings in the three microhabitats were similar for all sampling periods. Only data for the April 1994 sampling period are displayed. Data were collected at the two study sites, Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

Table 2.21. Spatial heterogeneity of adult *T. insignis* and *T. erectus* plants and seedlings, as measured by variance to mean ratios. Seedling counts were made in both Area 1 and 2 over three years (1992, 1993 and 1994), at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain) (n = 100 1 X 1 m quadrats per treatment). There were four (May 1992, August 1993, November 1993 and April 1994) sampling periods for *T. insignis* and three (December 1992, August 1993 and April 1994) sampling periods for *T. erectus*.

Species	Spatial heterogeneity within quadrats							
	Adults		Dead adults		Seedlings		Dead seedlings	
	Area							
	Area 1	Area 2	Area 1	Area 2	Area 1	Area 2	Area 1	Area 2
T. insignis								
Sampling time 1	3.30	3.77	*	*	2.44	0.96	-	-
Sampling time 2	2.34	2.86	1.19	*	1.74	3.72	-	-
Sampling time 3	1.47	9.79	1.37	*	8.44	19.15	-	-
Sampling time 4	2.13	1.94	1.45	*	0.25	0.26	8.10	4.09
T. erectus								
Sampling time 1	0.69	0.69	*	0.96	0.99	2.79	-	-
Sampling time 2	1.90	1.11	1.65	0.99	1.00	3.58	-	-
Sampling time 3	1.11	1.42	1.00	*	3.58	2.36	-	-

* no variance to mean ratios can be calculated on these data due to zero mean and variance values.

- no dead seedling data were collected at this sampling period.

Table 2.22. Temporal heterogeneity of adult *T. insignis* and *T. erectus* plants and seedlings, as measured by variance to mean ratios. Seedling counts were made in both Area 1 and 2 over three years (1992, 1993 and 1994), at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain) (n = 100 1 X 1 m quadrats per treatment). There were four (May 1992, August 1993, November 1993 and April 1994) sampling periods for *T. insignis* and three (December 1992, August 1993 and April 1994) sampling periods for *T. erectus*.

Species	Temporal heterogeneity					
	Adults		Dead adults		Seedlings	
	Area					
	Area 1	Area 2	Area 1	Area 2	Area 1	Area 2
T. insignis	54.94	23.22	10.16	*	609.20	226.25
T. erectus	2.99	8.10	1.75	2.71	3.91	2.25

* no variance to mean ratios can be calculated on these data due to zero dead adults.

Table 2.23. Estimates of numbers of plants or propagules per m^2 of area for *T. insignis* and *T. erectus*, at various stages of their life cycles, at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).[a]

Life cycle stages	T. insignis				T. erectus			
	Unharvested			Harvested	Unharvested			Harvested
	1992	1993	Average	1993	1992	1993	Average	1993
Adult plants:								
Male	0.54±0.22	0.51±0.26	0.53±0.24	0.32±0.15	0.41±0.07	0.52±0.2	0.47±0.14	0.10±0.03
Female	0.67±0.33	0.62±0.32	0.65±0.33	0.46±0.27	0.63±0.18	0.8±0.44	0.72±0.31	0.32±0.05
Other	0.00±0.00	0.004±0.01	0.002±0.005	0.96±0.51	0.07±0.04	0.04±0.01	0.06±0.03	0.43±0.11
Total	1.20±0.55	1.13±0.56	1.17±0.56	1.73±0.59	1.10±0.27	1.35±0.63	1.23±0.45	0.85±0.13
Annual total seed production	18494±4364	8642±2539	13568±3451	415±161	6077±830	13290±3762	9683±2296	69±16
Annual plump seed production [b]	17345±4093	7948±2335	12647±3214	294±114	5656±773	12755±3611	9206±2192	48±11
Seed bank sizes:								
i) Physical separation technique [c]								
Before dispersal	208±424	3058±4779	1633±260	1522±1759	321±549	1946±4738	1134±2644	1253±1452
After dispersal	3480±6066	4066±5987	3773±6027	1387±2162	2586±4275	2474±2689	2530±3482	429±618
ii) Seedling emergence technique								
After dispersal	1019±1074	1070±1281	1045±1178	102±322	713±548	815±644	764±596	51±161
Seedlings:								
May 1992	0.05±0.22			0.08±0.44	-			-
December 1992	-			-	0.24±0.82			0.02±0.14
August 1993	0.39±1.21			0.34±0.77	0.12±0.66			0.01±0.10
November 1993	3.07±7.67			5.23±6.65	0.23±0.74			0.08±0.27
April 1994	5.54±9.19			10.65±16.44	-			-

a All estimates are summarized from results presented in this chapter.

b Assuming constant ratios of aborted, predated and plump seed (using data from this study - see Table 2.7) throughout both unharvested and harvested areas at both study sites, in any one year.

c A seasonal fluctuation in seed bank size was observed.

Table 2.24. Actual and predicted seed loss for unharvested *T. insignis* and *T. erectus* populations at various stages of their life cycles. Data are estimates of actual numbers of plump seed per m^2 (unless otherwise stated), predicted and actual percentage plump seed loss and differences between actual and predicted percentage seed loss at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).[a] Data are a) from seed production (1992 and 1993) to incorporation into the seed bank, b) from incorporation of seed (1992) into the seed bank to twelve months later and c) from seed production (1992) to approximately twelve months later.

a All estimates are summarized from results presented in this chapter.

b Assuming constant ratios of aborted, predated and plump seed (using data from this study - see Table 2.7) throughout both study sites, in any one year.

c Assuming constant culm removal rates and plump seed production within the entire study site and from year to year.

d Difference between post-dispersal and pre-dispersal estimates (i.e. number of seeds per m^2 buried deeply) (using data from this study - see Table 2.13).

e Difference between post-dispersal (i.e. current year's seed and older seed) and pre-dispersal (i.e. only seed older than current year's seed) seed bank estimates (using data from this study - see Table 2.14).

f Percentage loss of seed from the seed bank was estimated using experimental seed banks in both burial boxes and burial bags (boxes / bags) (using actual data from the study - see Figure 2.6).

g Difference between estimated pre-dispersal (1993) and post-dispersal (1992) (i.e. number of seeds per m^2 buried deeply) (using actual data from the study - see Table 2.13). There was no net gain in deeply buried seed with time for *T. erectus*, therefore, no estimate of seed loss due to burial could be made.

	T. insignis			T. erectus		
a) From seed production to incorporation into the soil seed bank:						
	1992	1993	Average	1992	1993	Average
Annual total seed production	18493	8642	13568	6077	13291	9684
Loss: Pre-dispersal abortion	1.51 %	2.23 %	1.87 %	6.49 %	2.98 %	4.74 %
Loss: Pre-dispersal predation	4.70 %	5.81 %	5.26 %	0.44 %	1.05 %	0.75 %
Total pre-dispersal seed loss	6.21 %	8.04 %	7.13 %	6.93 %	4.03 %	5.48 %
Annual plump seed production [b]	17345	7948	12647	5656	12755	9206
Loss: Culm removal [c]	0.88 %	1.91 %	1.40 %	0.00 %	0.00 %	0.00 %
Loss: Post-dispersal predation	0.00 %	0.00 %	0.00 %	0.00 %	0.00 %	0.00 %
Loss: Burial [d]	0.41 %	6.15 %	3.28 %	5.04 %	0.32 %	2.68 %
Predicted total seed loss	1.29 %	8.06 %	4.68 %	5.04 %	0.32 %	2.68 %
Annual plump seed gain to seed bank	3273	1008	2141	2265	528	1397
Actual total seed loss [e]	81.13 %	87.32 %	84.23 %	61.32 %	95.86 %	78.59 %
Difference (actual - predicted)	79.84 %	79.26 %	79.55 %	56.28 %	94.91 %	75.60 %
b) From incorporation into the soil seed bank to twelve months later: [f]						
Loss: Predation	5.54 % / 4.58 %			2.20 % / 0.96 %		
Loss: Total germination	10.88 % / 4.25 %			2.87 % / 0.00 %		
Failed germination	2.50 % / 4.04 %			2.27 % / 0.00 %		
Seedlings	8.39 % / 0.21 %			0.60 % / 0.00 %		
Loss: "Lost"	16.54 % / 4.29 %			2.53 % / 1.44 %		
Loss: Burial [g]	20.00 %			-		
Predicted total seed loss	52.96 % / 33.12 %			7.60 % / 2.40 %		
Actual total seed loss	12.15 %			24.75 %		
Difference (actual - predicted)	- 40.81 % / - 20.97 %			17.15 % / 22.35 %		
c) From seed production (1992) to approximately twelve months later:						
Predicted grand total seed loss	54.25 % / 34.41 %			22.19 % / 27.39 %		
Actual grand total seed loss	93.28 %			86.07 %		
Difference (actual - predicted)	39.03 % / 58.87 %			63.88 % / 58.68 %		

Table 2.25. Actual and predicted seed loss for unharvested and harvested *T. insignis* and *T. erectus* populations at various stages of their life cycles. Data are estimates of actual numbers of plump seed per m^2 (unless otherwise stated), predicted and actual percentage plump seed loss and differences between actual and predicted percentage seed loss in 1993, at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).[a] Data are a) from seed production (1993) to incorporation into the seed bank, b) from incorporation of 1993 seed into the seed bank to twelve months later and c) from seed production (1993) to approximately twelve months later.

a All estimates are summarized from results presented in this chapter.

b Assuming constant ratios of aborted, predated and plump seed (using data from this study - see Table 2.7) throughout both study sites, and for any one harvesting treatment.

c Assuming constant culm removal rates and plump seed production within the entire unharvested area of the study site. Rates were not estimated for harvested areas.

d Difference between post-dispersal and pre-dispersal estimates (i.e. number of seeds per m^2 buried deeply) (using data from this study - see Table 2.13).

e Difference between post-dispersal (i.e. current year's seed and older seed) and pre-dispersal (i.e. only seed older than current year's seed) seed bank estimates (using data from this study - see Table 2.14). For harvested populations, of both study species, there was a net loss of seed with time, despite input of the current year's seed.

f Percentage loss of seed from the seed bank was estimated using experimental seed banks in both burial boxes and burial bags (boxes / bags) (using actual data from the study - see Figure 2.6). It is assumed that annual seed loss from the seed bank is constant with time and is similar for both harvested and unharvested areas.

g Difference between estimated pre-dispersal (1993) and post-dispersal (1992) (i.e. number of seeds per m^2 buried deeply) (using data from this study - see Table 2.13). There was no net gain in deeply buried seed with time for *T. insignis* (harvested area) and *T. erectus* (both unharvested and harvested area), therefore, no estimate of seed loss due to burial could be made.

	T. insignis			T. erectus		
	Unharvested	Harvested	Magnitude difference	Unharvested	Harvested	Magnitude difference
a) From seed production to incorporation into the soil seed bank:						
Annual total seed production	8642	415	20.82 X	13291	69	192.62 X
Loss: Pre-dispersal abortion	2.23 %	10.60 %	4.75 X	2.98 %	22.84 %	7.66 X
Loss: Pre-dispersal predation	5.81 %	18.55 %	6.22 X	1.05 %	7.84 %	7.47 X
Total pre-dispersal seed loss	8.04 %	29.15 %	3.63 X	4.03 %	30.68 %	7.61 X
Annual plump seed production [b]	7948	294	27.03 X	12755	48	265.73 X
Loss: Culm removal [c]	1.91 %	-	-	0.00 %	-	-
Loss: Post-dispersal predation	0.00 %	-	-	0.00 %	-	-
Loss: Burial [d]	6.15 %	90.84 %	14.77 X	0.32 %	approximately 100 %	1153.56 X
Predicted total seed loss	8.06 %	90.84 %	11.27 X	0.32 %	approximately 100 %	1153.56 X
Annual gain to seed bank [e]	1008	- 135	7.47 X	528	- 824	1.56 X
Actual total seed loss	87.32 %	approximately 100 %	1.15 X	95.86 %	approximately 100 %	1.04 X
Difference (actual - predicted)	79.26 %	9.16 %		95.54 %	approximately 0 %	95.54 X
b) From incorporation into the soil seed bank to twelve months later: [f]						
Loss: Predation	5.54 % / 4.58 %			2.20 % / 0.96 %		
Loss: Total germination	10.88 % / 4.25 %			2.87 % / 0.00 %		
Failed germination	2.50 % / 4.04 %			2.27 % / 0.00 %		
Seedlings	8.39 % / 0.21 %			0.60 % / 0.00 %		
Loss: "Lost"	16.54 % / 4.29 %			2.53 % / 1.44 %		
Loss: Burial [g]	20.00 %	-	-	-	-	-
Predicted total seed loss	52.96 % / 33.12 %	32.96 % / 13.12 %	1.61 X / 2.52 X	7.60 % / 2.40 %	7.60 % / 2.40 %	1 X / 1 X
c) From seed production (1993) to approximately twelve months later:						
Predicted grand total seed loss	61.02 % / 41.18 %	approximately 100 %	1.64 X / 2.43 X	7.92 % / 2.72 %	approximately 100 %	12.63 X / 36.76 X

2.6 DISCUSSION

Seed bank dynamics

The size of the soil-stored seed bank for a particular species, at any moment in time, is dependent upon several compounding factors. These include the presence of a pre-existing seed bank, seed inputs (recruitment from the seed rain and immigration of seed), dispersion and redistribution of seeds within the soil profile, and seed losses to emigration, germination, predation, inherent seed decay or pathogen attack, and death of emergent seedlings (Harper 1977, Cook 1980, Parker and Kelly 1989, Simpson *et al.* 1989). Variations in the microenvironment has considerable effect on these factors and, thus, these factors vary on a spatial and temporal scale (Leck *et al.* 1989, Parker *et al.* 1989).

All methods of seed bank estimation showed that the seed banks of both study species were large, with that of the non-sprouter (i.e. *T. insignis*) being larger than that of the sprouter (i.e. *T. erectus*). Similar results have been found for other non-sprouting and resprouting congenerics (Keeley 1977, Kelly and Parker 1990). *Thamnochortus insignis* seeds are smaller in size than those of *T. erectus*, thus fitting into the general trend of smaller seeded species forming larger seed banks and larger seeded species forming smaller seed banks (Parker and Kelly 1989). The larger *T. insignis* seed bank is likely to be due to the larger seed input, rather than to any other factor. Seed bank sizes of both species were positively related to seed input. Seed banks of both species were smaller and remained constant over two years relative to the much larger and more variable seed inputs. Unfortunately comparisons between soil seed banks of analogous species in different fire-prone mediterranean climate vegetation types are limited. Meney *et al.* (1994) reported post-dispersal seed bank sizes of up to 16 fold smaller (234 seeds per m^2) than those reported in this study for dominant Australian Restionaceae species. Meney and co-workers also found no difference between the estimated annual viable seed input and the seed bank for all

species studied except one. Research on shrub species has also reported variable seed production between years (Keeley 1977, 1987; Kelly and Parker 1990, Pierce 1990), as well as seed production exceeding seed bank size in many species (Keeley 1977, 1987; Musil 1991, Pierce and Cowling 1991b, Kilian and Cowling 1992). Seed production has also been found to vary in vegetation of different ages (Auld 1987) or at different sites (Lamont 1985). However, Pierce (1990) and Keeley (1987a) found the seed banks of several perennial shrub species to be relatively stable over a three year period in fynbos and over a ten year period in chaparral. As a result of this potential variation and its effect on seed bank sizes and dynamics, seed bank studies should ideally be continued for more than two years and for a number of differently aged *Thamnochortus* populations. *Thamnochortus insignis* is characterized by high seed production (13568 seeds per m^2), whereas *T. erectus* is characterized by a lower level of seed production (9684 seeds per m^2). Similar results have been found for other non-sprouting and resprouting congenerics (Keeley 1977, Cowling *et al.* 1987a). A large percentage (> 93%) of the seeds produced by both species are presumed to be viable (i.e. are plump). Population recruitment of both species will, thus, only be limited if pre- and post-dispersal seed losses are high enough to prevent the accumulation of a seed bank large enough to exploit available "safe sites" for germination, seedling establishment and development to reproductive maturity (Neser and Kluge 1986). High seed production, therefore, does not imply that any variation in seed numbers is inconsequential (Janzen 1969).

If the mass of annual seed production per plant is taken as a measure of reproductive effort (Harper *et al.* 1970), then the reproductive effort of *T. insignis* was higher (1.03 times) than that of *T. erectus*. This is despite the smaller size of *T. insignis* seeds compared to those of *T. erectus*. For a set amount of resources, a plant may allocate the resources in one of two ways: it either produces smaller amounts of larger seed, or larger amounts of small seed (Harper 1977). In this way the net cost to the parent plant of a smaller seeded species may thus be similar to that of a larger seeded

species. This is, however, not the case with *T. insignis* and *T. erectus*. It must, however, be borne in mind that the maintenance of dormant buds in sprouters requires a supply of carbohydrates, which like starch-rich seeds also have a cost to the plant (Meney *et al.* 1990a, 1990b; Pate *et al.* 1990, 1991; Bowen and Pate 1993). Some comparisons of seed production of non-sprouting and sprouting congenerics report expected increased reproductive effort among non-sprouters (Wells 1969, Meney *et al.* 1994), although many studies show no consistent pattern (Keeley 1977, 1987; Lamont 1985, Cowling *et al.* 1987a, Kelly and Parker 1990). Parker and Kelly (1989) provide a possible explanation. The authors suggests that because the seedling establishment environment places strong selection on seedlings of the same life-form regardless of whether the adults resprout, selection at this stage in the life history may mask other selective divergences.

Seed losses for both species were highest before incorporation into the seed bank than at any other stage in the life cycle. This was indicated by the large difference between the numbers of seed produced and the numbers of seed in the soil seed bank after dispersal. Large seed losses (up to 99%) during this period have also been observed for some fynbos (Pierce 1990, Kilian 1991) and chaparral (Keeley 1977) shrub species. Estimates of seed loss during this stage were larger for *T. insignis* (84.23%) than for *T. erectus* (78.59%). The seed banks of both species were not completely depleted over the year following seed input and, thus, there must be a persistent portion to the seed bank of both species. This was indicated by a large portion of the seed banks still existing shortly before new seed input. In both species, it appears that the majority of seeds in the seed bank enter and survive intact in the soil for more than one year (persistent portion), while fewer seeds enter and become depleted in numbers or remain in a viable condition for only one year (transient portion) (Grime 1979, Thompson and Grime 1979). The persistent soil seed bank of both species may be classified as type IV using the classification system of Thompson and Grime (1979). In this type of seed bank, few seeds germinate before they become incorporated into the seed bank. The length of time seeds reside in the soil seed bank is

determined by their physiological properties, including germination, dormancy, and viability, by the surrounding environmental conditions and subsequent changes in these conditions, and by the presence of seed predators and pathogens. Seed bank densities for *T. insignis* decreased from 3480 to 3058 per m^2 (12.15%) following one year's burial. *Thamnochortus erectus* seed bank densities decreased from 2586 to 1946 per m^2 (24.75%) following one year's burial. Meney *et al.* (1994) report larger (91-100% over two years) seed losses due to decay for dominant Australian Restionaceae species. This type of decline is expected in areas with strong seasonality, when seed bank samples are collected after peak seed production and dispersal and again shortly before the following seed production period. Further evidence for persistent seed banks in both species was provided by the results of the burial experiment. Results indicate that the seed banks in both species diminish steadily after replenishment, reaching a smaller size after 12 months. Seed losses for *T. insignis* (Burial boxes: 52.96%; burial bags 33.12%) are larger than for *T. erectus* (Burial boxes: 7.60%; burial bags 2.40%) over the 12 month period, regardless of the type of experimental seed bank used. Losses from the experimental seed bank are also much larger for *T. insignis* and much smaller for *T. erectus* after 12 months burial in the experimental seed banks than actually occurs in the field. This is surprising, considering that the burial experiment was conducted at the same time as the natural seed losses were monitored in the field, the experimental seed banks were completely "closed" to seed immigration and emigration, the environmental conditions experienced in the experimental seed banks were similar to those experienced in natural seed banks and the seed placed in the environmental seed banks were from the same seed crop, as were incorporated into the natural soil seed banks. There is no obvious explanation except that losses due to either predation, germination or decay must have been abnormally high, since losses due to emigration and deep burial are excluded from the experimental seed banks. For this reason, the experimental seed bank and the "seed budget" results must be viewed with some degree of caution. Generally, however, it was felt that trends were obvious and conclusions reached were well founded.

Pre-dispersal and post-dispersal seed loss

Seed bank studies should be designed to investigate all the processes responsible for both pre- and post-dispersal seed depletion to gain a full understanding of factors involved (Kremer 1993). These processes will be discussed in the following section.

Many of the seeds produced by both species were empty (i.e. lacked endosperm), despite the fact that the seed coat remained intact. Abortion may be due to maternal control in response to environment (cf. Gutterman 1980) or resource limitation, lethal genetic recombinations in outcrossers or unsuccessful pollination (Wiens *et al.* 1987). Predation levels for both species are low, therefore the production of large quantities of empty seeds to satiate predators and increase the chances of escaping predation (Pierce 1990), can be discounted for both species.

Seed predation has been shown to influence the input, survival, dispersion, composition, and longevity of soil-stored seeds in fire-prone Mediterranean-climate shrublands, including fynbos (Keeley and Hays 1976, Louda 1983, Bond and Slingsby 1984, Bond and Breytenbach 1985, Parker and Kelly 1989). Seed predation, thus, has the potential to have a major impact on the reproductive success, especially of non-sprouting species (see examples in Louda 1989). Indeed consumers at each stage of plant development can influence seed production and input to the seed bank. Traditionally, the analysis of predation in soil seed banks has only considered the fate of seeds already incorporated in the soil (Louda 1989). This study, however, attempted to assess the fate of seeds both before and after incorporation into the seed bank. Predation often contributes to heavy or variable seed losses of fynbos plants (Bond and Breytenbach 1985, Coetzee and Giliomee 1987, Pierce and Cowling 1991b). Pre- and post-dispersal predation levels measured for *T. insignis* (Pre-dispersal: 5.26%; Post-dispersal: 6.94%) and *T. erectus* (Pre-dispersal: 0.75%; Post-dispersal: 2.20%) in this study were extremely low. Pre-dispersal and post-dispersal predation in both species

reduced the magnitude of the initial viable seed crop, and hence both the build-up of seed in the soil and potentially the number of seed reaching "safe sites" (Janzen 1971). Considering the number of plump seeds produced annually by both species, it is doubtful whether it will have any effect on seedling recruitment. Isolated individuals may also be free from seed predation, and consequently able to contribute to population seed production (Auld and Myerscough 1986, Louda 1989). Predation of buried seed is thought to negligible (Thompson 1987). Despite this, moderate to high seed losses from the soil seed banks of many species have been observed (Bond and Breytenbach 1985, Kelly and Parker 1990, Kilian 1991), as well as for both study species. Andersen (1988) cautions that seed losses are usually underestimated because of the difficulty of assessing the total damage to seeds. The impact of predation on *T. insignis* and *T. erectus* populations will be greater on the initial seed production periods after fire, since the seed bank is severely reduced after fire (Section 3.6). For non-sprouters, such as *T. insignis* high seed loss at this time could be locally critical, should a fire occur. Persistence of hard-coated seed may be associated with a lower risk of mortality due to predation than seeds with a softer seed coat. Indeed, lower levels of seed predation were observed in this study for the harder coated *T. erectus* seed than for *T. insignis* seed.

Seed decay in the soil is another source of seed bank attrition (Harper 1977). Seed survival is dependent on complex deterioration resistance mechanisms, about which there exists little information. Contributing factors include features of the individual seed (such as seed coat structure), seed longevity, predators and microenvironmental conditions. Laboratory-stored plump seeds of both study species showed no decay after 18 months, suggesting that seed decay is not induced by pathogen infection during seed development and before seed release (cf. Benic and Knox-Davies 1983) or laboratory conditions were not conducive to pathogen growth. In the soil, however, pathogen activity has been implicated as a factor contributing to loss of seed viability prior to germination and in seed bank depletion, in many studies (see Kremer 1993 for review). Seed loss due to decay of dead

or germinating seed was higher in *T. insignis* (mean for boxes and bags = 16.54%) than for *T. erectus* (mean for boxes and bags = 2.53%), irrespective of the type of experimental seed bank used. Auld (1986b) found no differences in the dormancy and viability between laboratory and field stored *Acacia* seed over 24 months. This may be a due to the fact that the species has a hard seed coat. There are no studies that distinguish between microbial attack causing dormant or germinating seed death and that occurring after seeds die, although this information would shed light into the overall importance of microorganisms in seed mortality. It is possible that microorganisms preferably colonize and decay seed that are inferior in quality, therefore only a small proportion of seeds in soil succumbs to attack.

Germination of persistent seeds does not readily occur under favorable conditions due to complex and varied dormancy traits (Baskin and Baskin 1989). Seeds of both study species had a high degree of dormancy (discussed later). Seeds of many herbaceous species in fire-prone mediterranean climate shrublands must remain dormant in the soil for periods of at least the length of the fire-interval (e.g. 4-40 years for fynbos). Seeds of woody species have been found to be viable after up to 200 years of burial (see Parker and Kelly 1989 for examples). Dormancy can be imposed physically by impermeable seed coats, which prevent moisture uptake and gas exchange necessary for germination, or physiologically through mechanisms inhibiting germination of the embryo (Cook 1980, Baskin and Baskin 1989). The dormancy of buried seeds may originally be primary (inherent) in the newly deposited seed, but may become secondary (imposed) with storage. Seeds in the seed bank can exhibit annual dormant/non-dormant cycles in which dormant seeds can become non-dormant and germinate if environmental factors are not limiting (Baskin and Baskin 1989). Seeds failing to germinate can re-enter dormancy and become non-dormant for potential germination the following season. Dormancy of seeds in soil can be broken by a number of factors which often act together. These factors can also change with burial depth. Such factors may include chilling

followed by warmer temperatures, availability of oxygen, light regimes (e.g. photoperiod and spectral quality and intensity) and release from chemical inhibitors, as well as the correct moisture and pH levels. Changes due to seed ageing may be an important aspect in seed dormancy and longevity of seeds in fire-prone Mediterranean shrublands (Parker and Kelly 1989). The proportion of dormant seeds in persistent seed banks is variable (Thompson and Grime 1979) and few studies (Hilbert 1987) have investigated how dormancy influences seed bank dynamics. Seed dormancy is not critical to the persistence of long-lived species, such as *T. erectus*, which show a high resistance to fire and increase in seed bank size between fires. In contrast, seed dormancy in species with short life spans, such as *T. insignis*, who may die out prior to a fire, is critical. The potential seed bank size is directly influenced by differences in longevity and the rate at which seed viability is lost. Some studies have observed stronger dormancy mechanisms for seeds of non-sprouting species than for seed of resprouting species (Wells 1969, Meney *et al.* 1994).

Seed bank losses to germination are widely reported in the literature (Cook 1980, Thompson 1987). Germination, emergence and survival of seeds and seedlings have been regarded as key processes in determining plant distribution and population structure (Grubb 1977, Mayer 1980-1981, Frost 1984, Bond 1984, Breytenbach 1984, Fenner 1987, Le Maitre 1988, Pierce 1990). Supporting evidence from this study includes the distribution of plant sizes (as indicated by tussock diameter and plant height).

Thamnochortus insignis seeds are lighter than *T. erectus* seeds, and this together with a greater plant height, may provide the species with an increased opportunity for germination to occur by allowing seed to reaching more "safe sites" than seeds of *T. erectus*. Other factors including site characteristics, micro-environment of the seed, seed characteristics, predation, competition and chance may all influence the number of seeds that successfully germinate and become new reproductive individuals (see Auld 1986a for examples). Two principle establishment environments exist

temporally within fynbos, namely undisturbed and disturbed fynbos. Undisturbed vegetation, has several stresses including low levels of resources such as space, light, water, and nutrients (Schlesinger *et al.* 1982), growth-inhibiting compounds, and high levels of predation (Breytenbach 1984). As a result, seedling establishment in this environment is spatially and temporally rare (Parker and Kelly 1989, Pierce 1990, Kilian 1991). Fire-disturbed vegetation has increased resources (Gill 1975, Stock and Allsopp 1992). Recruitment in this environment is regulated by the physical environment (e.g. availability of soil moisture, soil temperatures, soil salinity and photoperiod), which may be heterogenous at the scale of the seed (Harper *et al.* 1965, Harper 1977, Fowler 1988, Baker 1989). Seedling germination and establishment in this environment often occurs *en masse* for many species (Kruger 1983). Thus, there is a strong selection for persistent seed banks in order to maximize recruitment in "open" environments after fires (Givinish 1981, Lamont *et al.* 1991). Germination cues appear to be specific and are related to environmental changes experienced after disturbance (Chapter 3) (Parker and Kelly 1989). Continuous seedling recruitment, during inter-fire years, has been observed for species with persistent seed banks in other periodically-burned ecosystems (Zammit and Westoby 1987, Parker and Kelly 1989, Keeley 1992). Some species, including *T. insignis*, are able to recruit both immediately after fire and during inter-fire years. Germination in mature vegetation during autumn and winter has been identified as a primary cause of seed loss from the seed bank for *T. insignis* (10.88% over 12 months of burial). In contrast, Meney and co-workers (1994) reported low inter-fire seedling recruitment of the dominant Australian Restionaceae studied. Although seedling recruitment for *T. insignis* was highly variable between years, seedlings were on average more numerous than the parent plants in mature vegetation. I suggest that the reason for the common inter-fire seedling recruitment observed in mature *T. insignis* populations is the favorable establishment environment (i.e. numerous "open" spaces) (Silvertown and Smith 1989). I predict that in older, denser *T. insignis* stands few seedlings will be recruited, due to more unfavorable environment

for germination and seedling survival. As the vegetation becomes increasingly senescent and gaps become larger, seedling recruitment levels may once again increase. Germination in mature vegetation during autumn and winter has been identified as a cause of small amounts of seed loss from the seed bank of *T. erectus* (2.87% over 12 months of burial). *Thamnochortus erectus* had relatively stable seedling recruitment from year to year and adult plants were more numerous than seedlings in mature vegetation. Recruitment in this species is primarily by sprouting and, thus, dependence on seedling recruitment is not great. Adult plant requirements are different from those of seeds or seedlings, and significant or complete prevention of inter-fire recruitment of species from the seed bank has been observed, in the presence of a plant canopy (Van der Valk and Davis 1978, Meredith 1985), as well as litter or a dense field layer (Van der Valk 1986, Facelli and Pickett 1991a, 1991b). Circumstantial evidence points to the germination of *T. insignis* being cued by the large temperature fluctuations near the soil surface. Such temperature fluctuations are experienced in exposed soil in vegetation gaps and after vegetation removal (Thompson *et al.* 1977), and not under fynbos vegetation (Appendix B). This was indicated by the ready germination of seeds from soil samples collected from the study sites in the controlled environment chamber, as well as increased germination following disturbance (Chapter 3), and the concentration of seedlings in gaps in mature vegetation. Increased seedling recruitment in the "open" microhabitat could also be the result of reduced fungal pathogen attack of seeds or seedlings (Augspurger 1984), or the favourable change in the light quality (Solangaarachchi and Harper 1987), or allelopathic effects of the shrub canopy or differential seedling survivorship due to differences in microsite characteristics. The reason for the low seedling recruitment observed under harvested thatch may be that the thatch creates a microenvironment experiencing decreased light, lower soil temperatures and increased moisture levels, which adversely effect seed survival and germination (Vazquez-Yanes *et al.* 1990). Thatch may also have a smothering effect on emerging seedlings (Grime 1973, 1979).

The actual mechanism by which dormancy is broken, remains unknown for both study species, thus, detailed germination studies are needed to validate these suggestions. Field experiments, as well as laboratory experiments on both young and old seed collected from both the plants and soil seed banks should ideally be conducted. It would also have been useful to place burial boxes and burial bags in specific microhabitats as this would have given an indication if a specific microhabitat favoured germination. This study did not provide information on pre-germination seed distribution in the different microsites, but it is reasonable to assume that seeds were abundant under vegetation as well as in gaps, although differences in densities may exist.

The probability of mortality at seedling stage is great (Harper 1977, Cavers 1983, Fenner 1987), making this one of the most vulnerable stages in a plant's life cycle (Harper and White 1974). Seedling survival was low for both study species. This greatly reduces numbers of plants surviving to adulthood. Indeed intermediate plants of both study species were rare in mature vegetation. Observations indicate that many of the emergent seedlings, especially for *T. insignis*, die over the hot, dry and windy summer months (Appendix B). Many other studies have found moisture stress to be the critical factor limiting early seedling survival (Purdie 1977, Auld 1987, Kilian 1991). For *Thamnochortus* seedlings to survive they are likely to need a deep enough root system to survive the dry period, as well as a certain amount of moisture at critical times. Clumped *T. insignis* seedlings may also undergo density-dependent mortality. This was, however, unlikely for *T. erectus* seedlings as they were widely spaced (Harper and Ross 1972). Herbivore damage (Breytenbach 1984, Midgely 1988), fungal disease and toxic substances have also been found to be a major causes of seedling death. Permanently marked quadrats, where seed input could be prevented, would have been useful in determining natural emergence of seedlings, seedling survivorship and fecundity from an existing seed bank. Natural seedling emergence would have also shed light on the contribution of buried seed to seedling recruitment. Monitoring of tagged seedlings at regular

intervals for a few years would increase the understanding of the factors responsible for seedling death. Exclosures could also be used to determine the effects of herbivory. Competition experiments in the field or nursery would increase our understanding of the role of density-dependent seed, seedling and adult mortality of both species.

The majority of seeds enter the soil passively and then continually move between surface and deeper soil layers. Although, burial may enable seeds to avoid surface-foraging predators, dehydration and the rapid loss of viability and survive fires; long-term ecological consequences are not fully understood (Cheplick and Quinn 1987, Parker and Kelly 1989). Seeds buried deeply will not experience the same environmental conditions as seeds near the soil surface. Deeply buried seeds not receiving the appropriate germination cues are effectively "lost" from the seed bank. In habitats, such as fynbos, where fire is an important disturbance factor, distribution of seeds within the soil is, thus, critical for survival (Auld 1986c, Parker and Kelly 1989). Seedlings are also often unable to emerge from deep soil depths and hence die (Section 2.5.6, Pierce 1990). Although some studies do exist (Auld 1986c, Pierce and Cowling 1991b) little is known about seed burial and seedling emergence depths of fynbos species, both of which are important aspects of seed bank dynamics (Parker *et al.* 1989). Changes in the proportions of *T. insignis* and *T. erectus* seeds in the shallow and deep soil cores were observed during the study period and seed loss to deep burial was estimated using these data. As expected, the majority of seeds were limited to the surface soil layers immediately after dispersal, and with time became more evenly dispersed throughout the soil profile. The majority of seeds of both species were found in the upper 10 cm of the soil profile, which is consistent with findings from other seed bank studies (Roberts 1981, Auld 1986b, Bigwood and Inouye 1988, Kilian 1991). Vertical movement of seeds in the soil depends on a number of factors, such as seed size and other morphological features, seed longevity and environmental factors, such as soil texture and structure, soil decomposition and compression, presence of cracks in the soil due to heat,

presence of litter, earthworm and other animal activity, wind and rainfall (Parker and Kelly 1989, Parker *et al.* 1989, Bertiller and Coronato 1994), which differ in relative importance among habitats. Vertical movement of seeds in seed banks has been recorded for some species (Kelly 1986).

Seed bank clumping

At the scale of the two areas within the general study sites, both seed production, seed banks and seedling recruitment were relatively homogeneous. This is probably due to the fairly homogeneous adult population structure observed for both species. At a smaller scale, however, both seeds and seedlings were highly clumped both on a horizontal and a vertical scale. Plant habitats are spatially diverse. For this reason, the spatial heterogeneity of a population's seed bank, both horizontally and vertically, can be critical for seedling establishment and survival. It would have been useful to determine the extent to which heterogeneity in the study sites influenced *Thamnochortus* seed and seedling dynamics (see Kalisz 1991). Clumping has been widely observed for both seeds (Thompson 1986, Fowler 1988, Pierce 1990, Kilian 1991) and seedlings (Keeley and Keeley 1981, Bond 1984, Pierce 1990, Kilian 1991). This is expected as seeds of both species would initially be dispersed around source individuals (Harper 1977, Howe 1986), and then factors such as wind and animal activity would cause variation within this initial distribution of seeds, resulting in non-random distribution of seed in the seed bank (Auld 1986b). Seed crop size, timing of dispersal, dispersal characteristics of the seed, and variations in environmental conditions (Parker *et al.* 1989) can all effect the initial post-dispersal spatial distribution of seeds and consequentially habitats that are available for seedling establishment (Leck *et al.* 1989, Parker *et al.* 1989). The winged seeds of both species are small and light, facilitating movement of seed on the soil surface after dispersal. It is likely that factors such as the prevailing wind direction and speed, disturbance to the soil surface and barriers to seed movement (e.g. *Thamnochortus* tussocks, other plants or burnt plant remains) are an important influence

on seed distribution patterns (Harper *et al.* 1965, Eckert *et al.* 1986). The medium to fine textured soil particles at the study sites are likely to be removed with seeds lying on the surface or in the upper soil layers, during the dry and windy summer months (Chambers *et al.* 1990, 1991). Seed predation and related activities of predators (Parker and Kelly 1989), germination (Garwood 1989, Parker and Kelly 1989) and seed decay patterns (Baker 1989, Baskin and Baskin 1989) may also be variable. Spatial variations in seed germination can be a result of depressions in the soil surface acting as "safe sites" for seed germination and establishment (*sensu* Harper 1977), allelopathic inhibition of seed germination under certain species, variations in the spectral composition of the incident radiation filtering through the canopy and variations in the soil temperature (Thompson *et al.* 1977, Brits 1986, 1987). Observations of reduced clumping of *T. insignis* seedlings in harvested vegetation, where seeds and seedlings experience a similar spectral composition and soil temperature fluctuations (Appendix B), appears to support the last two suggestions. More detailed studies, especially germination studies are needed to validate these suggestions. The increased clumping of *T. insignis* seeds and seedlings compared to *T. erectus* may be a consequence of greater seed production, higher seed predation, removal of whole culms to rodent nests and the more complex germination requirements in the species.

Long-term persistence of seed banks

While seasonal persistence of *T. insignis* and *T. erectus* seed banks appears certain, long-term persistence (for longer than 10 years) is uncertain. Both study species are able to produce large quantities of seed in the first few years of seed production and a small annual build up of the seed bank in these years is certain. Productive seasons responsible for the build-up of a large seed bank in both species are important to guard populations against short-term fire risks. These include protection against fire in all seasons and against low seed production in some years, and in the case of *T. erectus* against the death of dormant buds during intense fires. The ability to

resprout makes *T. erectus* less reliant on a persistent seed bank than the non-sprouter, *T. insignis*. It is, thus, not surprising that *T. insignis* produces more seeds and has a larger and more stable seed bank than *T. erectus*. There is, however, a trend of increased plant senescence and reduction of seed production levels, especially in older *T. insignis* populations (pers. obs. in De Hoop Nature Reserve). In senescent populations, seed input to the seed bank would equal seed loss and accumulation of seed in the seed bank would cease. Eventually, seed input to the seed bank would be less than seed loss and the seed bank would decrease in size. The life span of *T. insignis* is relatively short (*ca.* 20 years), whereas that of *T. erectus* is relatively long (*ca.* > 100 years) (pers. estimation). If the life span of *T. insignis* is shorter than the fire cycle (*ca.* 4 to 40 years) and new recruits are largely limited to the post-fire period (as is the case in older populations - pers. obs.), then the ability of the seed banks to persist beyond the lifespan of the plant and through to the next fire is uncertain. The seed bank studies show that approximately 12% of *T. insignis* seed are lost annually. It would, thus, take approximately nine years without new seed input, for the seed bank to be completely depleted. The seed burial experiments, however, give a less conservative estimate and show that approximately 50% of *T. insignis* seed in the seed bank are lost annually. Using these data, it would take approximately two years, without new seed input, for the seed bank to be completely depleted. These estimates assume that seed losses from the seed bank are constant. This may, however, not be the case. The seed loss in the first year of burial may represent the elimination of less hardy seed, with remaining seed being more resistant to decay (Holmes 1989). Long-term information on seed persistence is, however, not available for the study species. Ideally seed burial experiments needed to be continued for at least ten or more years, with more frequent evaluation of the seeds. The fact that the *T. insignis* seed banks do not attain extremely large sizes, despite years of extremely large annual seed inputs suggests that most seed survives only a few years, thus making populations vulnerable to local extinction as a result of long (*ca.* 50 year) fire intervals. Persistence of *T. insignis* soil-stored seed, therefore, has evolved to protect against relatively short-term fire risks

rather than long-term survival if the adult populations senesce. Pierce (1990) and Kilian (1991) also observed seasonally persistent soil-stored seed banks in non-sprouting fynbos shrub species. The long-term persistence of these seed banks were also uncertain. In chaparral, non-sprouting shrub species with a lifespan that is shorter than the fire cycle, often have seed that survives the full fire cycle of 50-100 years (Quick and Quick 1961, Keeley and Zedler 1978, Keeley and Keeley 1989, Keeley 1991, Parker and Kelly 1989). Non-sprouting species in fire-prone ecosystems that do have seasonally persistent seed banks are apparently dependent on the most recent years' seed inputs for post-fire recruitment (Keeley 1977, Zammit and Zedler 1988). The possibility of the fire cycle being longer than the lifespan of *T. erectus* is extremely low, therefore, persistence of soil-stored seed in this species would not have evolved to protect against long-term population survival. The continued spread of the *T. erectus* tussocks is a most effective way of maintaining populations during a long absence of fire. Data collected in this study suggests that most seed survives only a few years. Using data from the seed bank and seed burial experiments it is estimated that it would take approximately four to thirteen years, without new seed input, for the seed bank to be completely depleted. *Thamnochortus erectus* seed banks also do not attain extremely large sizes, despite years of moderate annual seed inputs. *Thamnochortus erectus* communities burn less frequently that those of *T. insignis* (Section 1.3). The evolutionary importance of a persistent seed bank is, thus, reduced in this long-lived resprouter compared to the short-lived non-sprouter, *T. insignis*. Weak persistence of *T. erectus* soil-stored seed has, therefore, evolved to protect against relatively short-term fire risks.

Consequences for fire

The presence of seasonally persistent seed banks suggests that the season in which fire occurs is not critical for the regeneration of the two study species. Large seasonal reductions in the seed bank size of both study species, however, indicates that fire in the season when seed bank levels are

at their lowest could result in lower seedling recruitment levels. Large numbers of seeds were present in the seed bank even prior to new seed input and this would ensure, at the very least, *T. insignis* population replacement. Population replacement of *T. erectus* is, however, uncertain (Section 3.6). Previous studies in fynbos have observed reductions in population recruitment of shrub species, as a result of fire in seasons when seed banks were at their lowest levels (Bond *et al.* 1984). Fire season may effect population replacement through the effect of fire season on seed germination and seedling survival of both study species (Bond *et al.* 1984, Le Maitre 1988). The probability of seed germination and seedling survival may be variable in different seasons due to varying environmental conditions. Fire season may also effect population replacement of the resprouter, *T. erectus*, through the adult plant survival. Fire in the season of new culm growth (during which carbohydrate reserves are mobilized and depleted) could potentially reduce adult plant survival, as reserve levels needed for regrowth after fire would not be available (Gill and Groves 1981).

Fire frequency can potentially have an impact on the population survival of both species, through its effects on seedling recruitment of the non-sprouter and adult plant survival of the resprouter. For non-sprouters it is critical that sufficient time should be allowed between fires for seed banks to accumulate to a level that would ensure self-replacement of the population (Keeley 1986, Pierce 1987, Hilbert 1987). *Thamnochortus insignis* has a juvenile period of approximately 4 years. The minimum time is uncertain, but it is likely to be at least several years after the plants reach reproductive maturity. Auld (1987) estimated that a further 6 years after reaching reproductive maturity is needed for the Australian species *Acacia suaveolens* and similar scenarios exist for species of other fire-prone vegetation types (Zedler *et al.* 1983, Fox and Fox 1986). Plant recovery after fire for the resprouter, *T. erectus*, is rapid (< 1 year) and seed production quickly reaches pre-fire levels (Section 3.5.1). It is, however, not known how long it takes plants to accumulate sufficient reserves for adult plants to withstand another fire. It is probable that the period of time needed is

shorter than that needed for accumulation of sufficient fuel reserves to support a fire. *Thamnochortus erectus* is, thus, better able to cope with short inter-fire periods than *T. insignis*.

Fire intensity plays an important role in population recruitment of both study species, through its effects on seedling recruitment of the non-sprouter and adult plant survival of the resprouter. From the population studies following fire (Chapter 3), it is suspected that fire related cues are the stimulus for breaking dormancy of seeds in *T. insignis*. It is unlikely that *T. insignis* seeds buried deeply in the soil will receive the same stimulus for breaking dormancy that seeds lying in the upper 1-2 cm of the soil's surface experience (Auld 1986c). As a result, even if it was physically possible for seedlings to emerge from deep burial and become established, germination and seedling establishment will not be initiated. *Thamnochortus insignis* seeds will be effectively lost from the population unless fires hotter than those usually needed are experienced, and then this would probably result in the death of seeds nearer the soil surface as a result of the high temperatures. For similar reasons, seed dispersal to ant nests deep in the ground is potentially hazardous to seeds, depending on the position of burial and the type of nest construction (Auld 1986b). High intensity fires could result in poor adult plant survival of *T. erectus* after fire due to the death of perenniating buds.

Fire recurrence intervals and seasonality are relatively predictable in fynbos (Van Wilgen 1984, Johnson and van der Wagner 1985), whereas fire intensity and post-fire climatic conditions are generally not (Kruger 1983, Christensen 1985, Cowling 1987). Actual experimental burning of populations of different ages and in different seasons may be the only way of adequately addressing how recruitment in the two study species varies with plant age since the last fire, fire season, fire intensity (especially on seed buried at different depths) and post-fire climatic conditions. An investigation into the pre- and post-fire seed bank dynamics would also be particularly

useful to gain a further understanding of the basic biology of the two species.

Consequences for thatch harvesting

The persistent seed banks of both *T. insignis* and *T. erectus* indicates that intense commercial harvesting of these species in one year would not deplete the seed bank. Seed bank estimates show that despite decreases in post-dispersal seed bank sizes after harvesting, seed banks of both study species still contained considerable numbers of seed. Harvesting does not result in drastic changes in the population structure of both study species, except for a reduction in average plant height and increase in the percentage of non-reproductive individuals, both of which return to pre-harvest levels within 1-3 years following harvesting (Section 3.5.2 and 3.6). Harvesting also results in higher levels of *T. insignis* seedling recruitment, possible due to increased seed input into the soil seed bank during harvesting (if this takes places during or immediately after the dispersal period) due to the dispersive action of harvesting. The creation of "open" spaces also encourages seedling recruitment as it provides the favoured microhabitat for seedling recruitment. The common practice of not harvesting very small or inaccessible adult plants and occasionally leaving a few unharvested culms ensures together with the extreme rapid regrowth and resumption of seed production within a year following harvesting, that there is some seed production during the year following harvesting (Section 3.5.2 and 3.6). Most of this seed, however, does not become incorporated into the germinable seed bank (Section 2.5.9). Seedlings are also not harvested and these together with resprouting adult plants will contribute increasing quantities of seed to the seed bank in the first 3-5 years following harvesting ((Section 3.5.2 and 3.6). From the findings of this chapter intense harvesting could be risked in the year preceding a planned burn for both species. However, the findings of chapter 3 suggest that this is not recommended for *T. erectus* (Section 4.1.3). Massive *T. insignis* seedling recruitment from buried soil-stored seed has been observed following fire, and population replacement is certain despite the death of all adult individuals

(Section 3.5.1 and 3.6). The majority of *T. erectus* adult plants survive fire and this together with moderate seedling recruitment from buried soil-stored seed will ensure population replacement (Section 3.5.1 and 3.6). However, repeated annual harvesting would deplete the seed bank. This study has shown that total seed production is severely reduced in the year following harvesting in both species. In both species, pre-dispersal seed losses due to predation and abortion are also higher for the seed crop following a harvesting event. This results in a dramatic reduction in the annual seed production and, therefore, the annual seed input into the seed bank. Losses of seed in the seed bank to deep burial were also higher following harvesting. From this study it is predicted all of the annual seed crop following harvesting will be lost from the seed bank in the year following seed input. Repeated harvesting would, thus, result in no annual increment of seed in the seed bank. Also sufficient time should be allowed after fire for seed banks of both species to accumulate before harvesting, as fire results in the reduction of seed bank size (Section 3.6, Kilian 1991). Harvesting also damages the harvested plant itself and all harvesting methods should take plant recovery into account. This is especially true for the non-sprouter *T. insignis*, which showed higher numbers of dead plants following harvesting than the resprouter (Section 3.5.2 and 3.6). Harvesting should be conducted shortly after seed dispersal and before the new culms reach the critical height (Section 1.4), as harvesting methods aid in seed dispersal and removal of young growing culms results in higher numbers of dead adult plants. Harvesting methods are also important for seedling recruitment in both species. All harvested thatch should be collected as seedling recruitment does not take place under thatch. If harvested in the way recommended in this study, mature populations of both species could be harvested approximately every five years to ensure sustainable utilization of the resource.

Methods of seed bank estimation

Estimates of seed bank size are affected by the site of sample collection, time of sample collection and differences in sampling methods, including sampling intensity and sampling technique (Parker and Kelly 1989). The recommended approach of collecting a large number of small sampling units rather than a few large ones for the same volume of soil sampled was used (Roberts 1981, Thompson 1986, Bigwood and Inouye 1988). Large numbers of sampling units are also used when seed aggregation (wind dispersal often results in clumps of seeds at a barrier to air flow) is probable (Goyeau and Fablet 1982). The total soil volume and the number of sampling units in this study is larger than the ranges commonly used for seed bank studies (Leck *et al.* 1989). Despite this, the large variation in the data, as is common in most seed bank studies, limits its value. According to the guidelines of Thompson (1986), the sample size was not adequate for obtaining statistically reliable estimates of seed bank size of both species (i.e. was not within 20% error of the mean). Further sampling to reduce variance was, however, not practical.

There have been a few published accounts of comparisons between the different methods of seed bank estimation (Pierce and Cowling 1991b, Manders 1990a). Two techniques are available to determine seed bank densities after samples are collected, namely physical separation and seedling emergence. Both techniques were used in this study, providing a more precise estimate of seed bank size than either technique alone (Conn *et al.* 1984). Both techniques have advantages and limitations. Most seed bank studies, however, use only the seedling emergence technique, with fewer studies using the physical separation technique and very few both. The reasons for the smaller estimate of seed bank size by germination than by direct seed counting are largely attributable to the nature of the two techniques.

Seedling emergence techniques provide an estimate of germinable seeds in the soil based on germination of seeds maintained under conditions favorable to germination (Thompson and Grime 1979, Roberts 1981, Gross 1990). These techniques are the least tedious and time consuming of the estimation methods, especially when dealing with small seeds, large sample sizes and multiple species (Roberts 1981, Gross 1990). The technique however, may underestimate viable, dormant seed abundances (Roberts 1981, Gross 1990) as an accurate reflection of germination cues supplied in the field (e.g. fire related cues) may be lacking (Mallik *et al.* 1984, Manders 1990a). Factors that prevent germination in undisturbed vegetation are unable to exert their influence in seedling emergence studies. To overcome this problem, the entire range of seasonal temperatures could have been used, as well as fire related cues. This was totally unpractical in this study. Furthermore, the exact germination requirements of the study species are not well understood. The seedling emergence technique may also give special emphasis to the transient component (Thompson and Grime 1979) of the seed bank and, therefore, bias results. Seedling emergence methods may have indicated a higher germinable seed bank density if the period of incubation was extended and stirring of the soil was more frequent. Seed numbers may also be underestimated as seeds may germinate but die before seedlings are counted. This is highly improbable for this study as seedlings were counted frequently. The technique is, thus, not sensitive as relatively small changes in the numbers of seeds may be masked by variable factors affecting seed germination and seedling mortality prior to monitoring. For these reasons, soil seed bank estimates for *T. erectus* and especially *T. insignis* with its complex germination cues (Section 3.6), using the seedling emergence technique, are probably underestimates.

In contrast, physical separation determines the total number of seeds in the soil, but gives no information about seed viability (Roberts 1981), which must be subsequently determined using germination, tetrazolium or other tests. Seed viability tests were not conducted in this study for the reasons given previously (Section 2.4.6.1). Physical separation is extremely tedious,

as it utilizes methods such as sieving and floating to physically separate seeds from the soil. Large-seeded species often show higher estimates by the physical separation technique than small-seeded species (< 1.5 mg). Pierce and Cowling (1991b), however, did not find this to be the case in six dune fynbos shrubs. The average *T. insignis* and *T. erectus* seed size were 1.017 mg and 1.546 mg, respectively. The physical separation technique was, thus, the most suitable method for this study, as the study species did not co-occur, seeds of both species were easily distinguishable and not too small in size and a high degree of sensitivity was required to detect seasonal variations in seed bank size.

This study supports the trend of higher seed bank estimates obtained by the physical separation than the seedling emergence technique (Roberts 1981, Vlahos and Bell 1986, Manders 1990a). Pierce and Cowling (1991b), however, found differing results for six dune shrubs and attributed the differences in estimates to seed bank size: species with larger seed banks having higher estimates by counting than species with fewer soil-stored seeds, which could be overlooked during seed counts. In this study, both study species had large seed banks, indeed several orders of magnitude larger than for those species with large seed banks studied by Pierce and Cowling (1991b). Therefore, the results of this study fit the hypothesis of Pierce and Cowling (1991b).

Viability estimates of seeds in the soil were made by comparing numbers of seedlings germinated from soil samples to number of plump seeds counted. This assumes that the conditions supplied in the controlled environment chamber completely broke dormancy in viable seeds and that all germinating seeds were counted as seedlings. Conditions in the controlled environmental chamber are similar to those conditions experienced by soil-stored seed during autumn and early winter in the upper few centimeters of soil in the south western Cape (Appendix B, Kilian 1991). Massive seedling recruitment has, however, been observed for *T. insignis* after fire and it is suspected that fire related cues may promote germination in this species.

For this reason, the viability estimate of approximately 28% for *T. insignis* are probably underestimated in this study. Viability estimates for *T. insignis* were higher than those of Singleton (1991), who germinated seeds on filter paper at the same temperature and light conditions as were used in this study. Estimated *T. insignis* seed viability was 3.3% for seeds collected from the inflorescences during the seed dispersal period and 8.7% for one year old seeds collected from the soil seed bank. This may indicate that storage of seed in the soil may play a role in the breaking of dormancy in the species. Viability estimates in this study were for seed that had been recently dispersed and incorporated into the seed bank. It is possible that estimates would have been higher if seed that had been buried for a period of time in soil seed bank had been used. The viability estimate of approximately 30% for *T. erectus* should be reliable. Evidence of high seed dormancy or low seed viability in both study species is the low numbers of seedlings observed in mature fynbos. Natural loss of seed viability during burial was not quantified for *T. insignis* and *T. erectus* in this study. Viability estimates of soil-stored seed of both species were similar to those of other fynbos species. Kilian (1991) estimated viability of soil-stored seeds of the shrub species, *Phylica* to be 35% and *Passerina* to be 50%, after fire. Confirmation of these results using other techniques of detecting seed viability (e.g. tetrazolium tests) would be useful.

Compared with other seed bank studies undertaken in the fynbos, this study has attempted to provided the most accurate representation of the seed bank dynamics of the study species by using a large number of samples and the simultaneous use of a number methods for estimating seed bank size and seed persistence/loss. The experimental approach was also useful in validating conclusions made from other observations.

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2.8 APPENDIX: DETAILS OF SOIL SAMPLE AREA AND VOLUME CALCULATIONS

Soil core area

Area of a circle = πr^2

Diameter of corer = 5 cm
Radius of corer = 2.5 cm

For the direct seed count experiment:
One sample = three soil cores

Area of one corer = $3.1415927 \times (2.5)^2$
$= 3.1415927 \times 6.25$
$= 19.634954\ cm^2$
or $= 0.001963\ m^2$

Area of three corers (one sample) = $3 \times 19.634954\ cm^2$
$= 58.904862\ cm^2$
or $= 0.005890\ m^2$

How many sample areas fit into 1 m^2 ground?
$= 1\ m^2 \div 0.00589\ m^2$
$= 169.77929$

therefore if x number of seeds are found in one sample
then the total number of seeds per m^2 ground in one sample
$= x \times 169.77929$ seeds per m^2 ground

For the seedling emergence technique:
One sample = one soil core

Area of one corer (one sample) = $3.1415927 \times (2.5)^2$

$= 3.1415927 \times 6.25$

$= 19.634954\ cm^2$

or $= 0.001963\ m^2$

How many sample areas fit into 1 m^2 ground?

$= 1\ m^2 \div 0.001963\ m^2$

$= 509.42435$

therefore if x number of seeds are found in one sample
then the total number of seeds per m^2 ground in one sample

$= x \times 509.42435$ seeds per m^2 ground

Soil core volume

Volume of a cylinder = $\pi r^2 h$

Diameter of corer = 5 cm
Radius of corer = 2.5 cm
Height of corer = 10 cm

For direct seed count experiment:
One sample = three soil cores

Volume of one corer = $3.1415927 \times (2.5)^2 \times 10$

$= 3.1415927 \times 6.25 \times 10$

$= 196.34954\ cm^3$

or $= 0.00019634954\ m^3$

Volume of three corers (one sample) = $3 \times 196.34954\ cm^3$

$= 589.04862\ cm^3$

or $= 0.0005889\ m^3$

How many sample areas fit into 1 m^3 ground?

= 1 m^3 ÷ 0.0005889 m^3

= 1698.0812

therefore if x number of seeds are found in one sample
then the total number of seeds per m^3 ground in one sample

= x X 1698.0812 seeds per m^3 ground

For seedling emergence technique:
One sample = one soil cores

Volume of one corer (one sample) = 3.1415927 X $(2.5)^2$ X 10

= 3.1415927 X 6.25 X 10

= 196.34954 cm^3

or = 0.00019634954 m^3

How many sample areas fit into 1 m^3 ground?

= 1 m^3 ÷ 0.00019634954 m^3

= 5094.2435

therefore if x number of seeds are found in one sample
then the total number of seeds per m^3 ground in one sample

= x X 5094.2435 seeds per m^3 ground

2.9 APPENDIX: DETAILS OF GENERALISED LINEAR MODELS

1) Total number of seeds - Pilot study:

Before harvesting

a) The model (Poisson distribution, log link) fitted to the total number of seeds found in 50 soil samples collected at two soil depths (referred to as depth; 1 = shallow; 2 = deep), at two sampling seasons (referred to as season; 1 = before dispersal; 2 = after dispersal) and over two years (referred to as year; 1 = 1992; 2 = 1993) for *Thamnochortus insignis* was:

$$\text{Log } \mu_{ijk} = \mu + \alpha_i^{\text{DEPTH}} + \beta_j^{\text{SEASON}} + \gamma_k^{\text{YEAR}}$$

μ_{ijk} = true count made in the ith soil depth, in the jth sampling season and in the kth year, $\alpha_1 = \beta_1 = \gamma_1 = 0$.

Analysis of deviance table:

Model	Residual deviance	D.F.	Deviance change	D.F. change
Mean	1453.70	7		
Mean + Depth	705.59	6	748.10	1
Mean + Depth + Season	113.68	5	591.90	1
Mean + Depth + Season + Year	54.12	4	59.56	1

Chi squared goodness of fit for the model:

Model	Chi-sq. statistic	D.F.	Akaike's adj.
Mean	1627.00	7	1629.00
Mean + Depth	625.80	6	629.80
Mean + Depth + Season	103.60	5	109.60
Mean + Depth + Season + Year *	48.39	4	56.39

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

Model	Parameter estim.	S.E.	GLIM estimate
Mean	3.73	0.10	42
Depth 2	-2.32	0.11	4
Season 2	1.92	0.1	285
Year 2	0.51	0.07	69

The residuals showed no pattern and none were excessively large.

b) The model (Poisson distribution, log link) fitted to the total number of seeds found in 50 soil samples collected at two soil depths (1 = shallow; 2 = deep), at two sampling seasons (1 = before dispersal; 2 = after dispersal) and over two years (1 = 1992; 2 = 1993) for *Thamnochortus erectus* was:

$$\text{Log } \mu_{ijk} = \mu + \alpha_i^{\text{DEPTH}}$$

μ_{ijk} = true count made in the ith soil depth, $\alpha_1 = 0$.

Analysis of deviance table:

Model	Residual deviance	D.F.	Deviance change	D.F. change
Mean	9.77	7		
Mean + Depth	2.50	6	7.27	1
Mean + Depth + Season	1.59	5	0.91	1
Mean + Depth + Season + Year	0.95	4	0.64	1

Chi squared goodness of fit for the model:

Model	Chi-sq. statistic	D.F.	Akaike's adj.
Mean	9.11	7	11.11
Mean + Depth *	2.10	6	6.10
Mean + Depth + Season	1.54	5	7.54
Mean + Depth + Season + Year	1.00	4	9.00

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

Model	Parameter estim.	S.E.	GLIM estimate
Mean	5.14	0.37	170
Depth 2	-2.70	1.46	12

The residuals showed no pattern and none were excessively large.

After harvesting

a) The model (Poisson distribution, log link) fitted to the total number of seeds found in 50 soil samples collected at two soil depths (1 = shallow; 2 = deep), at two sampling seasons (1 = before dispersal; 2 = after dispersal) and from two areas under different harvesting treatments (referred to as H.T.; 1 = harvested; 2 = unharvested) for *Thamnochortus insignis* was:

$$\text{Log } \mu_{ijk} = \mu + \alpha_i^{\text{DEPTH}} + \beta_j^{\text{SEASON}} + \gamma_k^{\text{HARVESTING TREATMENT}}$$

μ_{ijk} = true count made in the ith soil depth, in the jth sampling season and in the kth harvesting treatment, $\alpha_1 = \beta_1 = \gamma_1 = 0$.

Analysis of deviance table:

Model	Residual deviance	D.F.	Deviance change	D.F. change
Mean	1085.40	7		
Mean + Depth	532.23	6	553.10	1
Mean + Depth + Season	104.89	5	427.30	1
Mean + Depth + Season + H.T.	5.01	4	99.88	1

Chi squared goodness of fit for the model:

Model	Chi-sq. statistic	D.F.	Akaike's adj.
Mean	1307.00	7	1309.00
Mean + Depth	535.30	6	539.30
Mean + Depth + Season	101.20	5	107.20
Mean + Depth + Season + H.T. *	4.68	4	12.68

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

Model	Parameter estim.	S.E.	GLIM estimate
Mean	3.78	0.09	44
Depth 2	-1.91	0.10	7
Season 2	1.59	0.09	216
H.T. 2	0.69	0.07	88

The residuals showed no pattern and none were excessively large.

b) The model (Poisson distribution, log link) fitted to the total number of seeds found in 50 soil samples collected at two soil depths (1 = shallow; 2 = deep), from two areas under different harvesting treatments (1 = harvested; 2 = unharvested) and at two sampling seasons (1 = before dispersal; 2 = after dispersal) for *Thamnochortus erectus* was:

$$\text{Log } \mu_{ijk} = \mu + \alpha_i^{\text{DEPTH}} + \beta_j^{\text{HARVESTING TREATMENT}} + \gamma_k^{\text{SEASON}}$$

μ_{ijk} = true count made in the ith soil depth, in the jth harvesting treatment and in the kth sampling season, $\alpha_1 = \beta_1 = \gamma_1 = 0$.

Analysis of deviance table:

Model	Residual deviance	D.F.	Deviance change	D.F. change
Mean	8.47	7		
Mean + Depth	1.72	6	6.74	1
Mean + Depth + H.T.	0.84	5	0.88	1
Mean + Depth + H.T. + Season	0.83	4	0.02	1

Chi squared goodness of fit for the model:

Model	Chi-sq. statistic	D.F.	Akaike's adj.
Mean	8.14	7	10.14
Mean + Depth *	1.71	6	5.71
Mean + Depth + H.T.	1.05	5	7.05
Mean + Depth + H.T. + Season	1.00	4	9.00

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

Model	Parameter estim.	S.E.	GLIM estimate
Mean	5.09	0.37	162
Depth 2	-2.58	1.41	12

The residuals showed no pattern and none were excessively large.

2) Total number of seeds - Physical separation technique:

Before harvesting

a) The model (Poisson distribution, log link) fitted to the total number of seeds found in 150 soil samples collected over two years (1 = 1992; 2 = 1993) and at two sampling seasons (1 = before dispersal; 2 = after dispersal) for *Thamnochortus insignis* was:

$$\text{Log } \mu_{ij} = \mu + \alpha_i^{\text{YEAR}} + \beta_j^{\text{SEASON}}$$

μ_{ij} = true count made in the ith year and in the jth season, $\alpha_1 = \beta_1 = 0$.

Analysis of deviance table:

Model	Residual deviance	D.F.	Deviance change	D.F. change
Mean	4210.20	3		
Mean + Year	3229.10	2	981.10	1
Mean + Year + Season	1690.80	1	1538.30	1

Chi squared goodness of fit for the model:

Model	Chi-sq. statistic	D.F.	Akaike's adj.
Mean	2879.00	3	2881.00
Mean + Year	2679.00	2	2683.00
Mean + Year + Season *	1414.00	1	1420.00

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

Model	Parameter estim.	S.E.	GLIM estimate
Mean	6.89	0.02	984
Year 2	0.66	0.02	1901
Season 2	0.84	0.02	2274

The residuals showed no pattern and none were excessively large.

b) The model (Poisson distribution, log link) fitted to the total number of seeds found in 150 soil samples collected at two sampling seasons (1 =

before dispersal; 2 = after dispersal) and over two years (1 = 1992; 2 = 1993) for *Thamnochortus erectus* was:

$$\text{Log } \mu_{ij} = \mu + \alpha_i^{\text{SEASON}} + \beta_j^{\text{YEAR}}$$

μ_{ij} = true count made in the ith year and in the jth season, $\alpha_1 = \beta_1 = 0$.

Analysis of deviance table:

Model	Residual deviance	D.F.	Deviance change	D.F. change
Mean	2108.80	3		
Mean + Season	1143.70	2	965.10	1
Mean + Season + Year	866.02	1	277.70	1

Chi squared goodness of fit for the model:

Model	Chi-sq. statistic	D.F.	Akaike's adj.
Mean	1580.00	3	1582.00
Mean + Season	1030.00	2	1034.00
Mean + Season + Year *	788.00	1	794.00

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

Model	Parameter estim.	S.E.	GLIM estimate
Mean	6.68	0.03	795
Season 2	0.80	0.03	1774
Year 2	0.42	0.03	1208

The residuals showed no pattern and none were excessively large.

After harvesting

a) The model (Poisson distribution, log link) fitted to the total number of seeds found in 150 soil samples collected from two areas under different harvesting treatments (1 = harvested; 2 = unharvested) and at two sampling seasons (1 = before dispersal; 2 = after dispersal) for *Thamnochortus insignis* was:

$$\text{Log } \mu_{ij} = \mu + \alpha_i^{\text{HARVESTING TREATMENT}}$$

μ_1 = true count made in the ith harvesting treatment, $\alpha_1 = 0$.

Analysis of deviance table:

Model	Residual deviance	D.F.	Deviance change	D.F. change
Mean	26.84	3		
Mean + H.T.	2.03	2	24.81	1
Mean + H.T. + Season	1.00	1	1.03	1

Chi squared goodness of fit for the model:

Model	Chi-sq. statistic	D.F.	Akaike's adj.
Mean	26.85	3	28.85
Mean + H.T. *	2.02	2	6.02
Mean + H.T. + Season	1.00	1	7.00

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

Model	Parameter estim.	S.E.	GLIM estimate
Mean	7.16	0.59	1285
H.T. 2	0.90	0.19	3147

The residuals showed no pattern and none were excessively large.

b) The model (Poisson distribution, log link) fitted to the total number of seeds found in 150 soil samples collected at two harvesting treatments (1 = harvested; 2 = unharvested) and at two sampling seasons (1 = before dispersal; 2 = after dispersal) for *Thamnochortus erectus* was:

$$\text{Log } \mu_{ij} = \mu + \alpha_i^{\text{HARVESTING TREATMENT}} + \beta_j^{\text{SEASON}}$$

μ_{ij} = true count made in the ith harvesting treatment and in the jth season, $\alpha_1 = \beta_1 = 0$.

Analysis of deviance table:

Model	Residual deviance	D.F.	Deviance change	D.F. change
Mean	1553.60	3		
Mean + H.T.	428.48	2	1125.12	1
Mean + H.T. + Season	415.84	1	12.64	1

Chi squared goodness of fit for the model:

Model	Chi-sq. statistic	D.F.	Akaike's adj.
Mean	1363.00	3	1365.00
Mean + H.T.	412.50	2	416.50
Mean + H.T. + Season *	400.80	1	406.80

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

Model	Parameter estim.	S.E.	GLIM estimate
Mean	6.66	0.58	779
H.T. 2	0.97	0.61	2047
Season 2	-0.10	0.55	707

The residuals showed no pattern and none were excessively large.

3) Total number of viable seeds - Seedling emergence technique:

Before harvesting

The model (Poisson distribution, log link) fitted to the total number of viable seeds found in 10 soil samples collected for two species (referred to as species; 1 = *Thamnochortus insignis*; 2 = *T. erectus*) and over two years (1 = 1992; 2 = 1993) was:

$$\text{Log } \mu_{ij} = \mu$$

μ = true count.

Analysis of deviance table:

Model	Residual deviance	D.F.	Deviance change	D.F. change
Mean	1.87	3		
Mean + Species	0.16	2	1.71	1
Mean + Species + Year	0.03	1	0.13	1

Chi squared goodness of fit for the model:

Model	Chi-sq. statistic	D.F.	Akaike's adj.
Mean *	1.85	3	3.85
Mean + Species	0.16	2	4.16
Mean + Species + Year	0.03	1	6.03

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

Model	Parameter estim.	S.E.	GLIM estimate
Mean	2.88	0.12	18

The residuals showed no pattern and none were excessively large.

After harvesting

The model (Poisson distribution, log link) fitted to the total number of viable seeds found in 10 soil samples collected from two areas under different harvesting treatments (1 = harvested; 2 = unharvested) for two species (1 = *Thamnochortus insignis*; 2 = *T. erectus*) was:

$$\text{Log } \mu_{ij} = \mu + \alpha_i^{\text{HARVESTING TREATMENT}}$$

μ_1 = true count made in the ith harvesting treatment, $\alpha_1 = 0$.

Analysis of deviance table:

Model	Residual deviance	D.F.	Deviance change	D.F. change
Mean	35.16	3		
Mean + H.T.	1.02	2	34.14	1
Mean + H.T. + Species	0.11	1	0.90	1

Chi squared goodness of fit for the model:

Model	Chi-sq. statistic	D.F.	Akaike's adj.
Mean	30.13	3	32.13
Mean + H.T. *	1.01	2	5.01
Mean + H.T. + Species	0.11	1	6.11

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

Model	Parameter estim.	S.E.	GLIM estimate
Mean	0.41	0.58	2
H.T. 2	2.51	0.6	18

The residuals showed no pattern and none were excessively large.

4) Total number of seedlings:

a) The model (Poisson distribution, log link) fitted to the total number of seedlings per 100 1 X 1 m quadrats collected in three microhabitats (referred to as microh.; 1 = "open" 1993; 2 = under vegetation; 3 = under thatch), over three sampling periods (referred to as S.P.; 1 = Aug 1993; 2 = Nov 1993; 3 = April 1994) and from two areas under different harvesting treatments (1 = harvested; 2 = unharvested) for *Thamnochortus insignis* was:

$$\text{Log } \mu_{ijk} = \mu + \alpha_i^{\text{MICROHABITAT}}$$

μ_i = true count made in the ith microhabitat, $\alpha_1 = 0$.

Analysis of deviance table:

Model	Residual deviance	D.F.	Deviance change	D.F. change
Mean	11.06	17		
Mean + Microhabitat	3.65	15	7.41	2
Mean + Microhabitat + S.P.	0.69	13	2.96	2
Mean + Microh. + S.P. + H.T.	0.34	12	0.36	1

Chi squared goodness of fit for the model:

Model	Chi-sq. statistic	D.F.	Akaike's adj.
Mean	15.17	17	17.17
Mean + Microhabitat *	3.28	15	9.28
Mean + Microhabitat + S.P.	1.11	13	11.11
Mean + Microh. + S.P. + H.T.	1.00	12	13.00

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

Model	Parameter estim.	S.E.	GLIM estimate
Mean	5.98	0.50	395
Microhabitat 2	-2.80	2.06	24
Microhabitat 3	-6.16	10.74	1

The residuals showed no pattern and none were excessively large.

b) The model (Poisson distribution, log link) fitted to the total number of seedlings per 100 1 X 1 m quadrats collected in three microhabitats (1 = "open" 1993; 2 = under vegetation; 3 = under thatch), from two areas under

different harvesting treatments (1 = harvested; 2 = unharvested) and over three sampling periods (1 = Aug 1993; 2 = Nov 1993; 3 = April 1994), for *Thamnochortus erectus* was:

$$\text{Log } \mu_{ijk} = \mu + \alpha_i \text{MICROHABITAT} + \beta_j \text{HARVESTING TREATMENT} + \gamma_k \text{SAMPLING PERIOD}$$

μ_{ijk} = true count made in the ith microhabitat, in the jth harvesting treatment and in the kth sampling period, $\alpha_1 = \beta_1 = \gamma_1 = 0$.

Analysis of deviance table:

Model	Residual deviance	D.F.	Deviance change	D.F. change
Mean	104.99	11		
Mean + Microhabitat	30.22	9	74.77	2
Mean + Microhabitat + H.T.	13.81	8	16.41	1
Mean + Microh. + H.T. + S.P.	6.22	7	7.58	1

Chi squared goodness of fit for the model:

Model	Chi-sq. statistic	D.F.	Akaike's adj.
Mean	124.50	11	126.50
Mean + Microhabitat	27.41	9	33.40
Mean + Microhabitat + H.T.	12.40	8	20.40
Mean + Microh. + H.T. + S.P. *	4.94	7	14.94

* = best fitting model by Akaike's criterion

The coefficients and standard errors for the final model:

Model	Parameter estim.	S.E.	GLIM estimate
Mean	0.91	0.41	2
Microhabitat 2	-2.62	0.60	< 1
Microhabitat 3	-12.77	56.07	< 1
H.T. 2	1.36	0.37	10
S.P. 2	0.87	0.33	6
S.P. 3	0.00	-	2

The residuals showed no pattern and none were excessively large.

CHAPTER 3

EFFECT OF DISTURBANCE ON MORTALITY, VEGETATIVE REGROWTH AND SEEDLING RECRUITMENT

3.1 ABSTRACT

Mortality, vegetative regrowth and seedling recruitment of two thatching reed species, namely *Thamnochortus insignis* Masters and *Thamnochortus erectus* (Thunb.) Masters (Restionaceae), were investigated after fire at the De Hoop Nature Reserve (southern Cape) and after harvesting on the Agulhas Plain (south-western Cape). The study species are both perennial hemicryptophytes each with a different regeneration mode, the former being a non-sprouter and the latter a resprouter. Data were collected 34 months after a summer fire for *T. insignis* and 20 months after a late-summer fire for *T. erectus*, and in both the first and second flowering season after harvesting.

No plants of both species escaped from being burnt. In contrast, a few plants of both species escaped harvesting. More *T. insignis* plants escaped harvesting than for *T. erectus*, possibly due to there being more small shrubs at the *T. insignis* site which act as refuges. Fire is an unselective disturbance type, whereas harvesting is generally selective with the majority of unharvested *T.erectus* individuals having a small tussock diameter.

Fire resulted in greater adult plant mortality than harvesting for both species. The decrease in pre- to post-disturbance adult plant density varied according to disturbance type for both species. *Thamnochortus erectus* plants killed by fire had predominantly small and medium tussock diameters. *Thamnochortus insignis* plants killed by fire included the entire range of tussock diameters. Harvesting selectively killed small plants in both species.

Establishment after fire was exclusively by seed for *T. insignis* and by both resprouting from a subterranean base and seed for *T. erectus*. As a result, they did not have similar frequencies of dead adults, resprouting adults and seedlings after fire. Establishment after harvesting for both species was by both resprouting from a subterranean base and from seed. They, however,

did not have similar frequencies of dead adults, resprouting adults and seedlings after harvesting. The study species also had different frequencies of dead adults, resprouting adults and seedlings after fire and harvesting.

Thamnochortus insignis plant densities before disturbance could easily be achieved despite high seedling mortality. *Thamnochortus erectus* plant densities before disturbance could not easily be achieved after fire, although they could easily be achieved after harvesting. Plant densities after fire were, however, similar to those in undisturbed vegetation and population replacement was likely.

Thamnochortus erectus rapidly produced both reproductive and unreproductive culms after fire. After harvesting, both species rapidly produced culms, although *T. erectus* produced significantly more culms per plant than *T. insignis*. *Thamnochortus insignis*, however, produced more reproductive culms than *T. erectus*. The number of culms, and particularly the number of reproductive culms per *T. insignis* plant increased significantly between the first and second flowering season after harvesting, which was not the case for *T. erectus*. The number of unreproductive unbranched culms per plant was larger in the first than in the second flowering season after harvesting for both species. After disturbance the majority of culms per plant were unreproductive, although this decreased rapidly from the first to the second season after harvesting for *T. insignis*. The majority of resprouting unreproductive culms were unbranched. For *T. erectus*, after fire, only plants in the largest tussock diameter size class had > 25% reproductive culms per plant. *Thamnochortus insignis* had a significantly greater plant height than *T. erectus*, which may together with greater quantities of lighter seed, give *T. insignis* a greater colonizing ability compared to *T. erectus*.

Resprouting plants of both species, independent of tussock diameter, mainly produced culms from the edge of the tussock and from all over the tussock. Moreover, many individuals resprouting from the entire base had

the majority of culms at the edge of the tussock. Thus, it appears that, especially for *T. erectus*, the majority of dormant buds are situated at the edge of the tussock.

This study provided evidence for massive (*T. insignis*) and low (*T. erectus*) seedling recruitment in the post-disturbance environment compared to low to moderate inter-fire recruitment for both species. *Thamnochortus insignis* seedling recruitment was not confined to the first post-fire germination season. Maximum seedling establishment was associated with the "open" disturbed environment, particularly the post-fire environment, indicating that in addition to fluctuating soil temperatures experienced in autumn, fire related effects may maximize germination of *T. insignis* seed. Detailed germination studies are needed to verify this. In contrast, *T. erectus* seedling density in the post-disturbance environment compared to those in mature vegetation before disturbance was two-fold larger after fire and four-fold less after harvesting, indicating that germination was not stimulated by environmental stimuli in the post-disturbance environment.

This study provides evidence that a single disturbance event increases the successful establishment of the non-sprouter, *T. insignis*, largely by massive seedling recruitment. *Thamnochortus insignis* is also able to resprout and resume seed production rapidly after harvesting. In contrast, a single disturbance event does not increase the successful establishment of the resprouter, *T. erectus*, and populations maintain themselves by vegetative regrowth. *Thamnochortus insignis* can be seen as a pioneer species and *T. erectus* can be seen as persistent species. Implications of results for commercial harvesting are also discussed.

Key words: fire, germination cues, harvest, population replacement, seedling recruitment, vegetative growth.

3.2 INTRODUCTION

Restioid fynbos is fire-prone and subject to recurrent fires at a 10 to 30 year interval, although frequencies can vary widely from four to greater than 40 years (Kruger 1983, Bond 1984, Kruger and Bigalke 1984, van Wilgen 1984, Cowling *et al.* 1987). In the last decade, the principle thatch species, *T. insignis* and *T. erectus*, have been increasingly harvested (i.e. brushcut) for use as thatching material. Thus, in addition to periodic fires, harvesting has become an important disturbance in the vegetation type (Bond 1984, Kruger and Bigalke 1984, Cowling *et al.* 1987, Ball 1991). The lack of understanding of the ecological effects of fire and harvesting and their wise use as management tools is a cause for concern.

Disturbance, which occurs on a wide variety of spatial and temporal scales, disrupts population structure, changes resources (such as light, space or nutrients), substrate availability and the environment (such as reduced competition, seed predation and seedling herbivory), and thereby contributes to vegetation dynamics in many ecosystems (Naveh 1975, Gill 1981a, Christensen 1985, White and Pickett 1985, Cowling 1987). The survival and expansion of plant populations is dependent on their ability to regenerate after disturbance. Fynbos species posses a wide array of traits (e.g. ability to resprout, disturbance stimulated seed release, seed germination and flowering) to cope with fire and this enables population maintenance in the face of recurrent disturbance (Van der Merwe 1966, Kruger 1983, Le Maitre and Midgley 1992). An understanding of the responses of species or trait-complexes in relation to varying components of fire or harvesting regimes, provide the basis for understanding the underlying patterns in vegetation dynamics and the predictive basis for improved management capability. The effect of disturbance on plant population structure and on regeneration of dominant species in mediterranean-type ecosystems are well known (Gill 1981a, 1981b; Gill and Groves 1981). In fynbos, however, previous research undertaken has been

mostly limited to shrub species (see Greyling and Davis 1989 for examples; Pierce 1990, Kilian 1991, Mustart and Cowling 1992).

Fire and harvesting directly damage plants. Species differ in their response to damage and survive as a result of one or more of a variety of regenerative modes (Gill 1981a, 1981b; Frost 1984, Kruger and Bigalke 1984). The non-sprouting and the resprouting alternatives could be characterized as "high risk" and "low risk" regeneration modes (Ellner 1987). Non-sprouters, such as *T. insignis*, are often killed by fire or harvesting and are dependent exclusively on seed reserves for their regeneration and population survival. These species are reliant on the availability of soil-stored seed or a large annual seed production to enable population expansion after fire. Resprouters, such as *T. erectus*, are rarely killed by fire or harvesting and regenerate vegetatively from buds that occur on subterranean organs (Naveh 1975, James 1984). Resprouters require only sufficient seed to offset mortality of parent plants and populations could be expected to decline only if senescent individuals are not replaced by new genets in the long term (Bradstock and Myerscough 1988). The advantages of resprouting include retention of an already established position, initiation of growth immediately after disturbance with first-year growth being much more rapid than that of seedlings and periodic rejuvenation without the risks of the seedling stage. These advantages, thus, eliminate self-competition and competition with seedlings of other species. The degree of post-disturbance resprouting depends on the season in which the disturbance occurs and its effects on the environmental conditions (Laude *et al.* 1961), the physiological and morphological effects of the disturbance itself (Jameson 1963), the intensity and frequency of the disturbance (Kayll and Gimingham 1965), plant age (Hobbs and Gimingham 1984), availability of carbohydrate reserves (Jones and Laude 1984, Rundel *et al.* 1987, Bowen and Pate 1993), the size and depth of the subterranean organ (Auld 1990), pre-disturbance biomass of the plant (Rundel *et al.* 1987, Malanson and Trabaud 1988), and competition by neighbouring plants (Villa and Terradas 1992, Villa *et al.* 1994).

Fire and harvesting reduce seed input into the seed banks. This seed is then no longer available for regeneration, especially after recurrent disturbance events. Both species studied here have seasonally persistent seed banks (Chapter 2). Thus, local extinction is not expected following a fire in the year after harvesting, even if plants produced no seed in that year. The impact of harvesting will, however, be reduced if plants are able to resprout rapidly and resume seed production and if the site is protected from fire for a number of years, so as to allow a soil-stored seed bank to accumulate, especially for the non-sprouter. The rate at which seed accumulation in the seed bank occurs is important, as fires in populations that have yet to establish a seed bank can bring about local extinction of fire-sensitive species (Bradstock and Myerscough 1981, Van Wilgen 1984). Clearly the practice of leaving a proportion of individuals unharvested is recommended, if populations of harvested plants are not to be severely depleted. High intensity harvesting could damage plants to the extent that they do not recover sufficiently to maintain seed bank levels in subsequent years.

Despite the commercial importance of thatching reed, no guidelines exist for managers of thatch stands as to the intensity and frequency at which fire and harvesting of the two species should occur. Managers and harvesters have their own management methods. There is, however, no scientific basis for their methodology, and conflicts of opinion exist. There exists no information concerning the effects of disturbance on the vegetation dynamics of the two species. Yet knowledge of the dynamics of these two species is necessary if these resources are to be managed on a sustainable basis. There is a need for a general predictive model of vegetation response to perturbation, such as fire and harvesting. For these reasons, the effect of fire and harvesting on the mortality, vegetative regrowth and seedling recruitment of *T. insignis* and *T. erectus* were compared, and the results related to the regenerative modes of the two species. It was postulated that disturbance would result in lower levels of mortality of adult plants of the resprouter compared to the non-resprouter. It was also postulated that the rate of culm and seed production would be higher for the resprouter species

after fire, and that seedling recruitment after disturbance would be higher for the non-resprouter than the resprouter.

The study addressed the following questions: (1) *How does fire and harvesting effect plant mortality of the study species?* (2) *Are there any differences in the ability of the study species to resprout after fire and harvesting?* (3) *How does fire and harvesting effect seedling establishment of the study species?*

In order to obtain the answers to the above questions, plants escaping disturbance were quantified and compared, to determine whether any particular sex or size class was better able to escape disturbance. Adult plant mortality and survival in the two study species was quantified and compared, to determine whether any sex or size class was more vulnerable to mortality after disturbance. Vegetative regrowth and seed production was quantified and compared, to determine whether any differences in the type or pattern of culm regrowth exists in the two study species. Seedling recruitment and population expansion after disturbance for both species was quantified and compared. The results for the two disturbance types were compared for both species.

3.3 STUDY SPECIES AND STUDY SITES

The restioids (herbaceous, rush-like perennials) *T. insignis* and *T. erectus* (Restionaceae) were selected for this study. A detailed description of the two study species can be found in Chapter 1 and their characteristics are summarized in Table 3.1. The fact that the species are both commercially harvested and differ in their regenerative mode after fire, contributed to their being chosen as study species. *Thamnochortus insignis* is a non-sprouter i.e. reproductively-mature plants are fire sensitive and regeneration is by soil-stored seed (Linder 1991). *Thamnochortus erectus* is a resprouter i.e. reproductively-mature plants survive fire by sprouting (Linder 1991). Both species recruit seedlings during inter-fire periods, as well as

immediately after fire. Both species have winged, wind-dispersed seeds, with *T. insignis* and *T. erectus* seeds being dispersed from late autumn (mid-April) to mid-winter (July), and in summer (November to March), respectively. Seeds produced each year contribute to the soil-stored seed bank. *Thamnochortus insignis* and *T. erectus* seedlings germinate in late winter (from July to August) and from mid-autumn to mid-winter (April to June), respectively. The two allopatric species are closely related.

The study species' response to fire and harvesting was investigated at two sites in the De Hoop Nature Reserve (southern Cape) and two sites on the Agulhas Plain (south western Cape), respectively (i.e. there was a study site for each species at each study area) (Figure 3.1). The study areas are approximately 64 km distance apart. Each study site comprised of an homogeneous area of approximately 200 X 200 m, situated in a much larger area of similar vegetation. Approximately half of the study sites were either burnt or harvested. For logistic reasons it was not possible to conduct both investigations at the same study site, for each species. For the same reason it was not possible to have replicate treatments nor could quadrats be interspersed in undisturbed or disturbed areas. The experimental design, therefore, involved subsampling a given population rather than true replication.

Using the same structural dominant system of Campbell (1985), the fynbos vegetation type at both study areas was classified as Dry Restioid Fynbos. This vegetation type is tall, dense restioland (> 60% restioid cover) with a sparse shrub stratum (< 30 %) (Campbell *et al.* 1981). At both *T. insignis* sites, small- and large-leaved, non-proteoid shrubs were common. Proteoids, graminoids (except the study species), forbs, geophytes, creepers, succulents and annuals were rare. At both *T. erectus* sites, large-leaved non-proteoid shrubs (dune thicket species) were common. Ericoid shrubs, other graminoids, forbs, geophytes, creepers, succulents and annuals were rare. Proteoids were absent. Members of the Poaceae were common at the Agulhas Plain site only and formed a dense field layer in places. The

Agulhas Plain sites were free of alien vegetation, whereas the De Hoop Nature Reserve sites had a few alien *Acacias*. As is typical of mediterranean shrublands, the study areas are subject to recurrent fires (Kruger 1984, Keeley 1986) usually in the dry summer and autumn months (Van Wilgen 1984).

The climate of both study areas is typical of the south-western Cape, namely mediterranean-type with cool wet winters and warm dry summers. Climatic data for the nearest weather station (Cape Agulhas) are shown in Figure 3.2. The climate is mild, relatively uniform and frost free, with a mean annual temperature of 17°C (calculated for the period 1961-1993; Department of Environment Affairs, unpublished data). Approximately 65% of the 460 mm of annual precipitation falls in the winter months (May-October). During the two years preceding and during the year in which data were collected for this study (i.e. 1991-1993), annual rainfall was higher than the mean annual rainfall for two years (1992 = 527.5 mm; 1993 = 631 mm) and lower than the mean annual rainfall for one year (1991 = 408.9 mm). Mean monthly temperatures ranged from 24°C in January to 15.9°C in July during the same period. The area is extremely windy with mean daily winds, usually easterly in direction, exceeding 300 km day^{-1} during the summer months (Deacon *et al.* 1992).

The fire study sites at the De Hoop Nature Reserve are approximately 3.75 km from the coast and are 27.5 km apart. Evidence, including the large fuel loads of surrounding unburnt vegetation and the charred remains of large woody shrubs, indicates that the fires at both study sites were intense.

The *T. insignis* site was situated on the original De Hoop farm (34° 28' 14"; 20° 25' 48") and was a level area on a sandy plain between a limestone ridge to the north and a barrier dune (recent sand) to the south. The grey medium textured sand was shallow (*ca.* 0.5 m) and structureless, and overlies Bredasdorp formation limestone. The soil had a pH of 7.90. The area had been burnt in February (summer) of 1991. Total percentage projected foliage

cover before the site was burnt was 72%, of which 58% comprised *T. insignis* cover. *Thamnochortus insignis* plants were fairly vigorous, with the majority of culms being green.

The *T. erectus* site was situated on the original farm Elandspad (34º 25' 28"; 20º 43' 4") and was a level area of deep sand between two low limestone ridges, which were barely exposed. The grey-brown medium textured sand was deep (*ca.* 1 m) and structureless, and overlies Bredasdorp formation limestone. The area had been burnt in April (end of summer) 1992. Total percentage projected foliage cover before the site was burnt was 65%, of which 25% comprised *T. erectus* cover. *Thamnochortus erectus* plants were fairly vigorous.

The harvested study sites on the Agulhas Plain are approximately 8.75 km from the coast and are 10 km apart. The *T. insignis* site was situated on the farm Zoetendalsvallei (34^0 44' 57"; 20^0 00' 9") and was a gently sloping area (< 10^0) on a small ridge. The shallow soils (*ca.* 90 cm) were structureless, unconsolidated, grey colluvial sands (Fernwood form) of mixed origin (calcareous sands or Table Mountain Group sandstone) (Thwaites and Cowling 1988). The soil was well-drained and overlies Bredasdorp formation limestone. The soil had a pH of 5.59. The vegetation community at Zoetendalsvallei was ten years old and was last burnt in 1981. Total percentage projected foliage cover before the site was harvested was 83%, of which 53% comprised *T. insignis* cover. *Thamnochortus erectus* plants were fairly vigorous.

The *T. erectus* site was situated on the farm Zeekoeivlei (34^0 39' 38"; 20^0 02' 35") and was a gently sloping area (< 10^0) on a small ridge. The shallow soils (*ca.* 50 cm) were well-drained, structureless, grey colluvial sands (Fernwood form) of mixed origin (calcareous sands or Table Mountain Group sandstone) (Thwaites and Cowling 1988). The unconsolidated older dune sand at the *T. erectus* site (Zeekoeivlei) was browner in colour, finer in texture and more fertile than those at the *T. insignis* site (Thwaites and

Cowling 1988). The sand overlies a hard orange-brown Table Mountain Group sandstone layer. The soil had a pH of 5.12. The vegetation community at Zeekoeivlei ranges from open to dense shrubland and was mature, being at least fifteen years old. Total percentage projected foliage cover before the site was harvested was 83%, of which 40% comprised *T. erectus* cover. *Thamnochortus erectus* plants were fairly vigorous.

3.4 METHODS AND MATERIALS

3.4.1 EFFECT OF FIRE

Field work was conducted in December 1993, 34 months after a summer fire at the *T. insignis* site and 20 months after a late summer fire at the *T. erectus* site. Three germination and plant growth seasons had passed since the fire for *T. insignis* and two germination and plant growth seasons had passed since the fire for *T. erectus*. At each site, 60 randomly placed 1 X 1 m quadrats were carefully searched for adult plants, burnt remains of adult plant tussock bases and seedlings. The tussock diameter of all adult plants or the remains of adult plants was measured, as well as the plant height. Plants were classified as unburnt or burnt. Burnt plants were classified either as dead or living. All living plants were further classified as male, female or "other" (i.e. sex undetermined). Resprouting burnt plants were classified according to the pattern of resprouting: resprouting over the entire base, resprouting from the edge of the base only or resprouting from the middle of the base only. If the plant was resprouting from the entire base, the percentage of culms resprouting from the edge was estimated. All culms of resprouting adult plants were counted and divided into the following categories: reproductive (i.e. bearing a current year's inflorescence), unreproductive unbranched (i.e. not bearing an inflorescence) or unreproductive branched culms. Seedling height, estimated age and microsite were determined.

Seedling and adult densities and adult to seedling ratios were calculated for post-fire vegetation, as well as for adjacent unburnt vegetation. Dispersion coefficients (variance : mean ratios) were calculated from seedling, dead and living adult counts (n = 60) and these were used as an index of the degree of contagion (non-random distribution) on a 1 X 1 m horizontal scale, for both study species.

The frequency of *T. insignis* and *T. erectus* individuals observed in the dead adult, resprouting adult and seedling categories were arranged in a contingency table and analyzed using the chi-squared statistic (Zar 1984). The null hypothesis was that the frequency of individuals in each category would be distributed in the same proportions, for each of the two species. The frequency of: burnt *T. insignis* and *T. erectus* individuals, *T. erectus* individuals which had culms resprouting from the entire base and from the edge of the base only and *T. erectus* resprouting reproductive and unreproductive culms observed in each of the tussock diameter categories were arranged in a contingency table and analyzed using the chi-squared statistic. Tussock diameter categories were combined to prevent a biased chi-square value resulting from expected frequencies < 1 and/or expected frequencies < 5 in more than one-fifth of its cells. Chi-square analyses could not be performed on the unburnt, burnt dead and living adult plant tussock diameter data due to the low frequency of individuals in the tussock diameter categories. The statistical computer programme Statgraphics 6.0 (STSC Inc.) was used for the chi-square analyses (Statgraphics 1987).

3.4.2 EFFECT Of HARVESTING

Both study species were harvested after the 1992 flowering season and before the following year's cohort of new culms had reached the critical height (Section 1.4). Both populations of the study species had culms of marketable length before harvesting. Techniques normally used to harvest thatch in the area were utilized (Section 1.4). Data were collected during the first (hereafter referred to as 1993) and second (hereafter referred to as

1994) flowering season after harvesting, for both study species. At each site, 100 randomly placed 1 X 1 m quadrats, in both the harvested and unharvested areas, were carefully searched for adult plants, harvested remains of dead adult plants and seedlings. The tussock diameter of all resprouting adult plants or the base of dead adult plants was measured, as well as plant height. Plants were classified as unharvested or harvested. Harvested plants were classified either as dead or living. All living plants were further classified as male, female or "other" (i.e. sex undetermined). Resprouting harvested plants were classified according to the pattern of resprouting: resprouting over the entire base, resprouting from the edge of the base only or resprouting from the middle of the base only. If the plant was resprouting from the entire base, the percentage of culms resprouting from the edge was estimated. All culms of resprouting adult plants were counted and divided into the following categories: reproductive (i.e. bearing a current year's inflorescence), unreproductive unbranched (i.e. not bearing an inflorescence) or unreproductive branched culms. Seedling height, estimated age and microsite were determined.

Seedling and adult densities and adult to seedling ratios were calculated for post-harvesting vegetation, as well as for adjacent unharvested vegetation. Dispersion coefficients (variance : mean ratios) were calculated from seedling, dead and living adult counts (n = 100) and these were used as an index of the degree of contagion (non-random distribution) on a 1 X 1 m horizontal scale, for both study species.

The frequency of: *T. insignis* individuals after fire and after harvesting (1994 data), harvested *T. insignis* and *T. erectus* individuals (1993 and 1994 data), harvested *T. insignis* individuals in 1993 and 1994 and harvested *T. erectus* individuals in 1993 and 1994 observed in the dead adult, resprouting adult and seedling categories were arranged in a contingency table and analyzed using the chi-squared statistic (Zar 1984). The null hypothesis was that the frequency of individuals in each category would be distributed in the same proportions. Chi-square analyses could not be performed on the *T. erectus*

fire data due to the low frequency of individuals in the dead adult and seedling categories. The frequency of: individuals of both species in a number of categories (i.e. unharvested and harvested, harvested dead and harvested live, which had culms resprouting from the entire base and from the edge of the base only) and resprouting reproductive and unreproductive culms observed in each of the tussock diameter categories were arranged in a contingency table and analyzed using the chi-squared statistic. Tussock diameter categories were combined to prevent a biased chi-square value resulting from expected frequencies < 1 and/or expected frequencies < 5 in more than one-fifth of its cells. Chi-square analyses could not be performed on some of the unharvested and dead adult plant tussock diameter data due to the low frequency of individuals in the tussock diameter categories. The statistical computer programme Statgraphics 6.0 (STSC Inc.) was used for the chi-square analyses (Statgraphics 1987).

For each of the two study species, paired t-tests were used to determine the significance of the effect of year on the number of resprouting culms (i.e. reproductive and unreproductive), the number of reproductive culms, the number of unreproductive unbranched culms and the number of unreproductive branched culms per plant. For each year, paired t-tests were used to determine the significance of the effect of species type on the number of resprouting culms (i.e. reproductive and unreproductive), the number of reproductive culms, the number of unreproductive unbranched culms and the number of unreproductive branched culms per plant. For each of the two study species, paired t-tests were used to determine the significance of the effect of year on plant height. For each of the two years, paired t-tests were used to determine the significance of the effect of species on plant height. The statistical computer programme Statgraphics 6.0 (STSC Inc.) was used for the t-tests (Statgraphics 1987).

3.5 RESULTS

A comparison of mortality, vegetative regrowth and seedling recruitment after disturbance (fire and harvesting) for the two study species, differing in their mode of post-fire regeneration, showed significant differences between species and disturbance type.

3.5.1 EFFECT OF FIRE

Adult adult plant densities in adjacent unburnt vegetation were 2.90 individuals per m^2 for *T. insignis* and 1.53 individuals per m^2 for *T. erectus*. No *T. insignis* or *T. erectus* plants escaped from being burnt (Figure 3.3).

The post-fire frequency of *T. insignis* and *T. erectus* individuals in the dead adult, resprouting adult and seedling categories was significantly different (X^2 = 826.9910, d.f. = 2, n = 889, $P < 0.001$), with *T. insignis* dead adults and seedlings (adults: 174 individuals (21.89%), seedlings: 621 individuals (78.11%)) being more frequent than *T. erectus* dead adults and seedlings (adults: 4 individuals (4.25%), seedlings: 2 individuals (2.13%)), and *T. erectus* resprouting adults (88 individuals (93.62%)) being more frequent than *T. insignis* resprouting adults (0 individuals (0%)).

All of the adult *T. insignis* plants were killed during the fire (Figure 3.4). Very few (4% of burnt plants) adult *T. erectus* plants were killed by the fire and all plants surviving the fire were resprouting from a subterranean base. Mean plant height at the time of sampling was 120.49 cm (n = 88). All dead *T. erectus* plants were of small (101-200 mm) and moderate (301-400 mm) tussock diameter (Figure 3.4). Living adult plant post-fire densities were 0 individuals per m^2 for *T. insignis* and 1.47 individuals per m^2 for *T. erectus*. The decrease in pre- to post-fire adult plant density was 100.00% for *T. insignis* and 3.92% for *T. erectus*.

The surviving *T. erectus* plants responded by producing culms, mainly from the edge (51% of all living burnt plants) and from all over (48% of all living burnt plants) of the tussock (Figure 3.5). Very few plants had culms growing from the middle of the tussock only (1% of all living burnt plants), and those that did had a small tussock diameter (Figure 3.5). Approximately 67% of the individuals that were resprouting from the entire base had 60-100% of culms at the edge of the tussock. The frequency of resprouting *T. erectus* individuals in the various tussock diameter categories was independent of pattern of resprouting (edge and all over only) (X^2 = 11.2760, d.f. = 9) (Figure 3.5).

At the time of sampling, there was an average of 9.7 reproductive culms (12% of total culms) and 70.8 unreproductive culms (88% of total culms) per *T. erectus* plant (n = 88) (Table 3.2). Unreproductive culms were made up of 60.3 of unbranched culms (85% of unreproductive culms) and 10.5 branched culms (15% of unreproductive culms) (Table 3.2). The frequency of resprouting *T. erectus* culms in the various tussock diameter categories was not independent of reproductive status (X^2 = 579.5390, d.f. = 13) (Figure 3.6). Plants of all tussock diameter size classes, except for the largest tussock diameter size class (i.e. 901-1000 mm), had > 75% unreproductive culms per plant (including both unbranched and branched culms) (Figure 3.6). Plants in the largest diameter size class had approximately even numbers of unreproductive and reproductive culms (Figure 3.6).

At the time of sampling, the sex of the minority (27%) of *T. erectus* plants was undetermined and the ratio of percentage male : female plants was 0.94.

Seedling densities in mature vegetation were 0.02 seedlings per m^2 for both *T. insignis* and *T. erectus*. Seedling : adult ratios were 0.01 for *T. insignis* and 0.01 for *T. erectus*. Post-fire seedling densities were 10.35 seedlings per m^2 for *T. insignis* and 0.03 seedlings per m^2 for *T. erectus*. The seedling :

adult ratio was 0.02 for *T. erectus*. Seedling : adult ratios could not be calculated for *T. insignis* due to the zero value for adult plants.

The *T. insignis* seedling to dead adult ratio of 3.57 indicated that plant densities before the fire could easily be achieved despite high seedling mortality. The *T. erectus* seedling to dead adult ratio of 0.50 indicated that plant densities before the fire could not be achieved after fire. Plant densities (i.e. including seedlings and adults) after fire were, however, similar to those in undisturbed mature vegetation.

Thamnochortus insignis average seedling height was 8.35 cm (n = 621) and the two *T. erectus* seedlings were 8.50 cm and 11.00 cm in height. *Thamnochortus insignis* seedlings had a large range in plant height (1.5-47.5 cm), suggesting that recruitment had occurred in all three winter seasons since the fire. The majority (96.62%) of *T. insignis* seedlings were in "open" areas between resprouting fynbos shrubs and few (3.38%) seedlings were under fynbos shrubs. The low numbers of *T. erectus* seedlings did not allow for any conclusions regarding recruitment.

The coefficients of variation (n = 60) were high (i.e. > 1) for *T. insignis* post-fire seedlings and dead adults (Table 3.3). This suggests that seedlings and dead adults are highly clumped at the scale of 1 X 1 m (Whittaker 1975, Zar 1984). There were no post-fire living adult plants. The coefficients of variation (n = 60) were low (i.e. < 1) for *T. erectus* post-fire seedlings and dead adults (Table 3.3). This suggests that seedlings and dead adults are evenly distributed at the scale of 1 X 1 m (Whittaker 1975, Zar 1984). The coefficient of variation (n = 60) was high (i.e. > 1) for *T. erectus* post-fire living adults (Table 3.3). This suggests that living adults are clumped at the scale of 1 X 1 m (Whittaker 1975, Zar 1984).

3.5.2 EFFECT OF HARVESTING

Pre-harvesting adult plant densities in mature vegetation were 2.48 individuals per m^2 for *T. insignis* and 1.59 individuals per m^2 for *T. erectus*. Fewer *T. erectus* (mean for 1993 and 1994 = 8 plants (i.e. 4.7% of total plants)) plants escaped harvesting, than for *T. insignis* (mean for 1993 and 1994 = 23 plants (i.e. 8.8% of total plants)). All unharvested *T. insignis* plants were 1-200 mm in diameter for both 1993 and 1994 data (Figure 3.7). The majority (1993: 76%, 1994: 24%) of unharvested plants were 1-100 mm in diameter, with a smaller percentage (1993: 24%, 1994: 37%) being 101-200 mm in diameter. These were also the tussock diameter size classes that had the majority of individuals (Figure 3.7), suggesting that the observation is a consequence of greater plant numbers in these size classes and that plants were randomly selected for harvesting. The majority of unharvested *T. erectus* plants were also confined to two tussock diameter size classes, which varied between years (Figure 3.7). In 1993 90% of unharvested plants were 1-100 mm in diameter and in 1994 80% of unharvested plants were 1-100 mm in diameter. In 1993 the remaining 10% of unharvested plants were 501-600 mm in diameter and in 1994 the remaining 20% of unharvested plants were 101-200 mm in diameter. These were not the tussock diameter size classes that had the majority of individuals (Figure 3.7), suggesting that the observation is not a consequence of greater plant numbers in these size classes, and that harvesting was selective.

The frequency of harvested *T. insignis* individuals in the various tussock diameter categories was not independent of year (X^2 = 42.1977, d.f. = 5) (Figure 3.7). The frequency of harvested *T. erectus* individuals in the various tussock diameter categories was independent of year (X^2 = 4.3930, d.f. = 13) (Figure 3.7). The frequency of unharvested *T. insignis* individuals in the various tussock diameter categories was not independent of year (X^2 = 13.7621, d.f. = 3) (Figure 3.7). For both *T. insignis* and *T. erectus*, the frequency of harvested individuals in the various tussock diameter

categories was not independent of species (1993: X^2 = 234.0190, d.f. = 13; 1994: X^2 = 208.5560, d.f. = 13) (Figure 3.7).

The frequency of *T. insignis* individuals in the dead adult, resprouting adult and seedling categories was significantly different after fire and harvesting (X^2 = 280.3210, d.f. = 2, n = 1583, P < 0.001), with dead adults being more frequent after fire (174 individuals (21.89%)) compared to after harvesting (11 individuals (1.40%)), and resprouting adults and seedlings being more frequent after harvesting (adults: 138 individuals (17.51%), seedlings: 639 individuals (81.09%)) compared to after fire (adults: 0 individuals (0%), seedlings: 621 individuals (78.11%)).

In both 1993 and 1994, the post-harvesting frequency of *T. insignis* and *T. erectus* individuals in the dead adult, resprouting adult and seedling categories was significantly different (1993: X^2 = 30.6287, n = 403; 1994: X^2 = 451.6190, n = 1474; d.f. = 2, P < 0.001), with *T. insignis* dead adults (1993: 23 individuals (9.09%), 1994: 19 individuals (1.45%)) and seedlings (1993: 34 individuals (13.44%), 1994: 1065 individuals (81.05%)) being more frequent than *T. erectus* dead adults (1993: 2 individuals (1.33%), 1994: 0 individuals (0%)) and seedlings (1993: 1 individuals (0.67%), 1994: 8 individuals (5.00%)); and *T. insignis* resprouting adults (1993: 196 individuals (77.47%), 1994: 230 individuals (17.50%)) being more frequent than *T. erectus* resprouting adults (1993: 147 individuals (98.00%), 1994: 152 individuals (95.00%)).

The post-harvesting frequency of *T. insignis* individuals in the dead adult, resprouting adult and seedling categories was significantly different in 1993 and 1994 (X^2 = 460.5290, d.f. = 2, n = 1567, P < 0.001), with dead adults being more frequent in 1993 (23 individuals (9.09%)) compared to 1994 (19 individuals (1.45%)), and resprouting adults and seedlings being more frequent in 1994 (adults: 230 individuals (17.50%), seedlings: 1065 individuals (81.05%)) compared to 1993 (adults: 196 individuals (77.47%), seedlings: 34 individuals (13.44%)).

The post-harvesting frequency of *T. erectus* individuals in the adult and seedling categories was not significantly different in 1993 and 1994 (X^2 = 4.1697, d.f. = 1, n = 310), with adults and seedlings being similar in 1993 (adults: 149 individuals (9.33%) and seedlings: 1 individual (0.67%)) compared to 1994 (adults: 152 individuals (95.00%) and seedlings: 8 individuals (5.00%)).

Thamnochortus insignis and *T. erectus* seedling death as a result of harvesting (i.e. trampling by harvesters and smothering by harvested thatch) was not quantified, although it is suspected to be low. A few (mean for 1993 and 1994 = 8.6% of harvested plants) adult *T. insignis* plants were killed by harvesting. Plants died immediately (within a few weeks) after harvesting and there was no increase in dead plants with time (pers. obs.). Very few (mean for 1993 and 1994 = 0.6% of harvested plants) adult *T. erectus* plants were killed by harvesting. The frequency of dead *T. insignis* individuals in the various tussock diameter categories was independent of year (X^2 = 2.4028, d.f. = 3), with all dead plants being 1-200 mm in tussock diameter (Figure 3.8). In 1993, the majority (61%) of dead plants were 1-100 mm in diameter, with a smaller percentage (39%) being 101-200 mm in diameter. In 1994, the majority (63%) of dead plants were 101-200 mm in diameter, with a smaller percentage (37%) being 1-100 mm in diameter. In 1993, all dead *T. erectus* plants were 1-300 mm in diameter, with 50% of dead plants being 1-100 mm in diameter and 50% of dead plants being 201-300 mm in diameter (Figure 3.8). No dead *T. erectus* plants were recorded in 1994. For both the 1993 and 1994 data, the frequency of living individuals in the various tussock diameter categories were not independent of species (1993: X^2 = 206.862, d.f. = 13; 1994: X^2 = 189.081, d.f. = 13) (Figure 3.8). Living plants were more evenly distributed amongst the diameter size classes for both species, but especially for *T. erectus* (Figure 3.8). For both *T. insignis* and *T. erectus* harvested individuals, the frequency of living individuals in the various tussock diameter categories was not independent of year (*T. insignis*: X^2 = 40.1572, d.f. = 5; *T. erectus*: X^2 = 40.8843, d.f. = 13) (Figure 3.8). The majority of living *T. insignis* plants were 1-200 mm in

diameter (1-100 mm: 45%, 101-200 mm: 41%) for the 1993 data and 101-200 mm in diameter (68%) for the 1994 data. The majority of living *T. erectus* plants were 301-500 mm in diameter (301-400 mm: 23%, 401-500 mm: 25%) for the 1993 data and 301-400 mm in diameter (24%) for the 1994 data. Post-harvesting adult plant densities were 1.96 individuals per m^2 for *T. insignis* and 1.47 individuals per m^2 for *T. erectus*. The decrease in pre- to post-harvesting adult plant density was 20.97% for *T. insignis* and 7.55% for *T. erectus*.

The surviving *T. insignis* plants responded by producing culms, mainly from all over the tussock (1993: 61% of all living harvested plants, 1994: 48% of all living harvested plants) and from the edge of the tussock (1993: 38% of all living harvested plants, 1994: 52% of all living harvested plants). Very few plants had culms growing from the middle of the tussock only (1993: < 1% of all living harvested plants, 1994: 0% of all living harvested plants). Many (1993: 32%, 1994: 30%) of the individuals that were resprouting from the entire base had 60-90% of culms at the edge of the tussock. In both 1993 and 1994, the frequency of resprouting individuals in the various tussock diameter categories was independent of resprouting pattern (1993: $X^2 = 3.3967$, d.f. = 5; 1994: $X^2 = 6.6771$, d.f. = 5) (Figure 3.9). For both plants resprouting from the edge and plants resprouting from all over the tussock, the frequency of resprouting individuals in the various tussock diameter categories was not independent of year ("Edge": $X^2 = 12.5910$, d.f. = 5; "All over": $X^2 = 23.5704$, d.f. = 5) (Figure 3.9).

Thamnochortus erectus plants responded by producing culms, mainly from the edge of the tussock (1993: 52% of all living harvested plants, 1994: 28% of total living harvested plants) and all over the tussock (1993: 48% of all living harvested plants, 1994 72% of all living harvested plants). No plants had culms resprouting from the middle only in 1993 or 1994 (0% of all living harvested plants). Many (1993: 49%, 1994: 54%) of the individuals that were resprouting from the entire base had 60-100% of culms at the edge of the tussock. In both 1993 and 1994, the frequency of resprouting

individuals in the various tussock diameter categories was independent of resprouting pattern (1993: X^2 = 19.6437, d.f. = 11; 1994: X^2 = 8.8028, d.f. = 11) (Figure 3.9). For both plants resprouting from the edge and plants resprouting from all over the tussock, the frequency of resprouting individuals in the various tussock diameter categories was independent of year ("Edge": X^2 = 0.5177, d.f. = 9; "All over": X^2 = 3.6649, d.f. = 11) (Figure 3.9).

In both 1993 and 1994, *T. erectus* had significantly more resprouting culms (i.e. both reproductive and unreproductive) per plant than *T. insignis* (1993: t = 13.1878, 1994: t = 6.8562, P < 0.001) (Table 3.4). In both 1993 and 1994, *T. insignis* had significantly more reproductive culms per plant than *T. erectus* (1993: t = 4.4931, 1994: t = 9.4817, P < 0.001) (Table 3.4). In both 1993 and 1994, *T. erectus* had significantly more unreproductive unbranched and branched culms per plant than *T. insignis* (unbranched: 1993 - t = 7.9395, 1994 - t = 4.4151; branched: 1993 - t = 14.9255, 1994 - t = 16.5863; P < 0.001) (Table 3.4). For *T. insignis*, the estimated number of resprouting culms per plant was significantly larger in 1994 than in 1993 (t = 10.0076, P < 0.001) (Table 3.4). For *T. erectus*, the estimated number of resprouting culms per plant was not significantly different in 1993 compared to 1994 (t = 0.5344) (Table 3.4). For *T. insignis*, the estimated number of reproductive culms, unreproductive unbranched culms and unreproductive branched culms per plant was significantly larger in 1994 than in 1993 (reproductive: t = 9.7207, P < 0.001; unreproductive unbranched: t = 6.6039, P < 0.001; unreproductive branched: t = 3.1596, P < 0.01) (Table 3.4). For *T. erectus*, the estimated number of reproductive culms and unreproductive branched culms per plant was not significantly different in 1993 compared to 1994 (reproductive: t = 0.7404, unreproductive branched: t = 1.4093) (Table 3.4). For *T. erectus*, the estimated number of unreproductive unbranched culms per plant was not significantly different in 1993 compared to 1994 (t = 0.6276) (Table 3.4).

In 1993, the frequency of *T. insignis* resprouting culms in the various tussock diameter categories was independent of reproductive status (X^2 = 1.5551, d.f. = 7) (Figure 3.10). However, in 1994, the frequency of resprouting culms in the various tussock diameter categories was not independent of reproductive status (X^2 = 32168.4000, d.f. = 9) (Figure 3.10). In both 1993 and 1994, the frequency of *T. erectus* resprouting culms in the various tussock diameter categories was not independent of reproductive status (1993: X^2 = 99.1678, d.f. = 11; 1994: X^2 = 24.3569, d.f. = 11) (Figure 3.10). For both reproductive and unreproductive culms of both species, the frequency of resprouting culms in the various tussock diameter categories was not independent of year (*T. insignis* reproductive: X^2 = 260.4840, d.f. = 9; unreproductive: X^2 = 513.0090, d.f. = 9; *T. erectus* reproductive: X^2 = 18.4430, d.f. = 9; unreproductive: X^2 = 156.2310, d.f. = 11) (Figure 3.10). In both 1993 and 1994, the frequency of resprouting reproductive culms in the various tussock diameter categories was not independent of species (reproductive 1993: X^2 = 1914.9100, d.f. = 7; 1994: X^2 = 546.9980, d.f. = 5; unreproductive 1993: X^2 = 8587.4500, d.f. = 12; 1994: X^2 = 10347.5000, d.f. = 12) (Figure 3.10).

In 1993, the sex of the majority of *T. insignis* (64%) and *T. erectus* (87%) plants were undetermined. The main reason for this was that few inflorescences were formed in the year following harvesting. In 1994, however, the sex of the minority (16%) of *T. insignis* plants were undetermined. The increase in the percentage reproductive plants between 1993 and 1994 was 49%. In 1994, this majority increased to 91% for *T. erectus* plants. The decrease in the percentage reproductive plants between 1993 and 1994 was 4%. The ratio of percentage male : female *T. insignis* plants was 0.56 in 1993 and 0.90 in 1994. The ratio of percentage male : female *T. erectus* plants was 0.73 in 1993 and 0.75 in 1994.

In both 1993 and 1994, *T. insignis* had a significantly greater plant height than *T. erectus* (1993: t = 9.1351, 1994: t = 13.3176, $P < 0.001$) (Table 3.5). For both *T. insignis* and *T. erectus* plant height was not significantly greater

in 1993 compared to 1994 (*T. insignis*: t = 0.1975, *T. erectus*: t = 1.6528) (Table 3.5).

0.39 seedlings per m^2, 1994: 5.54 seedlings per m^2) for *T. insignis* and 0.18 seedlings per m^2 (1993: 0.12 seedlings per m^2, 1994: 0.23 seedlings per m^2) for *T. erectus*. Seedling : adult ratios were 2.23 (1993: 0.23, 1994: 4.23) for *T. insignis* and 0.09 (1993: 0.05, 1994: 0.12) for *T. erectus*. Post-harvesting seedling densities were 5.50 seedlings per m^2 (1993: 0.34 seedlings per m^2, 1994: 10.65 seedlings per m^2) for *T. insignis* and 0.05 seedlings per m^2 (1993: 0.01 seedlings per m^2, 1994: 0.08 seedlings per m^2) for *T. erectus*. Seedling : adult ratios were 2.58 (1993: 0.17, 1994: 4.63) for *T. insignis* and 0.03 (1993: 0.01, 1994: 0.05) for *T. erectus*. The large increase in seedling density after harvesting for *T. insignis* (1.85 times; 1993: decreased 1.15 times, 1994: increased 1.92 times) and the large decrease in seedling density after harvesting for *T. erectus* (3.60 times; 1993: 12.00 times, 1994: 2.88 times) suggests that direct and/or indirect harvesting related cues break dormancy and stimulate germination of *T. insignis* and not *T. erectus* seed.

The *T. insignis* (32.68) seedling to dead adult ratio (1994 data) indicated that plant densities before harvesting could easily be achieved despite high seedling mortality. The *T. erectus* seedling to dead adult ratio could not be calculated due to the zero value for dead adults. Plant densities before harvesting could, however, be easily be achieved despite high seedling mortality.

In 1993, *T. insignis* average seedling height was 7.29 cm (n = 34) and the height of the *T. erectus* seedling was 6.99 cm. In 1994, *T. insignis* average seedling height was 1.72 cm (n = 1065) and *T. erectus* average seedling height was 6.29 cm (n = 8). The large decrease in average *T. insignis* seedling height indicates that a large number of seedlings were recruited in the 1993 germination season (i.e. the first germination season after harvesting). In

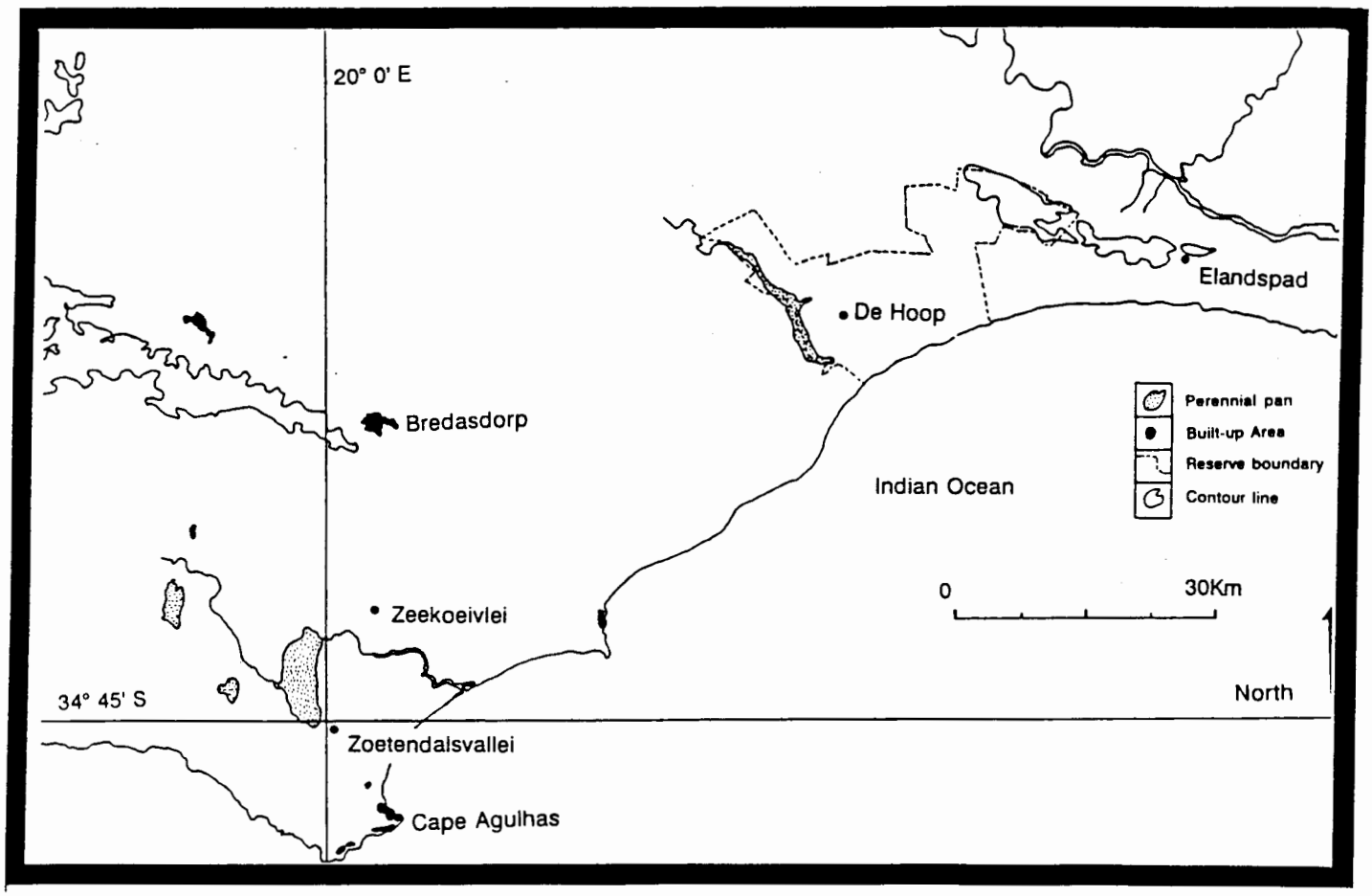
both years, *T. insignis* (1993: 0.25-18.0 cm, 1994: 0.10-21.00 cm) and *T. erectus* (1993: 0.20-12.00 cm, 1994: 0.20-11.30 cm) seedlings had a large range in plant height, suggesting that recruitment had not only occurred in the two years after harvesting. The majority (92.59%; 1993: 91.18%, 1994: 93.99%) of *T. insignis* seedlings were in "open" areas between resprouting fynbos plants (i.e. shrubs and *Thamnochortus* plants) and few (7.41%; 1993: 8.82%, 1994: 6.01%) seedlings were under fynbos plants. In both 1993 and 1994, all *T. erectus* seedlings (100%) were in "open" areas between fynbos plants.

The coefficients of variation (n = 100) were high (i.e. > 1) for *T. insignis* and *T. erectus* post-harvesting seedlings (*T. insignis*: 1993 only, *T. erectus*: 1994 only), living and dead adults (*T. erectus*: 1993 only) (Table 3.3), suggesting clumping at the scale of 1 X 1 m (Whittaker 1975, Zar 1984). The coefficients of variation were low (i.e. < 1) for *T. insignis* and *T. erectus* post-harvesting seedlings (*T. insignis*: 1994 only, *T. erectus*: 1993 only) and dead adults (*T. erectus*: 1994 only) (Table 3.3), suggesting an even distribution at the scale of 1 X 1 m (Whittaker 1975, Zar 1984).

Table 3.1. Characteristics of the study species, *Thamnochortus insignis* Masters and *Thamnochortus erectus* (Thunb.) Masters, Restionaceae.

Characteristic	Species	
	T. insignis	T. erectus
Distribution	Gouritz River mouth to west of Cape Agulhas	From Darling (near Malmesbury) to Knysna
Habitat	Coastal forelands, on young poorly developed sands (0.25-<1m) derived from Bredasdorp Formation limestone	Coastal forelands, on older, better developed sands
Plant height (m)	< 2.5 m	< 1.5 m
Pollination syndrome	Wind	Wind
Dispersal syndrome	Wind	Wind
Flowering	October to March (summer)	August to November (spring)
Pollination	February (summer)	August to September (spring)
Seed dispersal	April to July (autumn to winter)	August to September (winter to spring)
Seed germination	July to August (winter)	April to June (autumn to winter)
Vegetative growth	June to September (winter to spring)	April to May (autumn)
Harvesting	May to August (winter)	December to April (summer to autumn)
Post-fire response	Non-sprouter	Sprouter

Figure 3.1. Map indicating the location of the study sites: Zoetendalsvallei and Zeekoeivlei (Agulhas Plain), and De Hoop and Elandspad (De Hoop Nature Reserve).



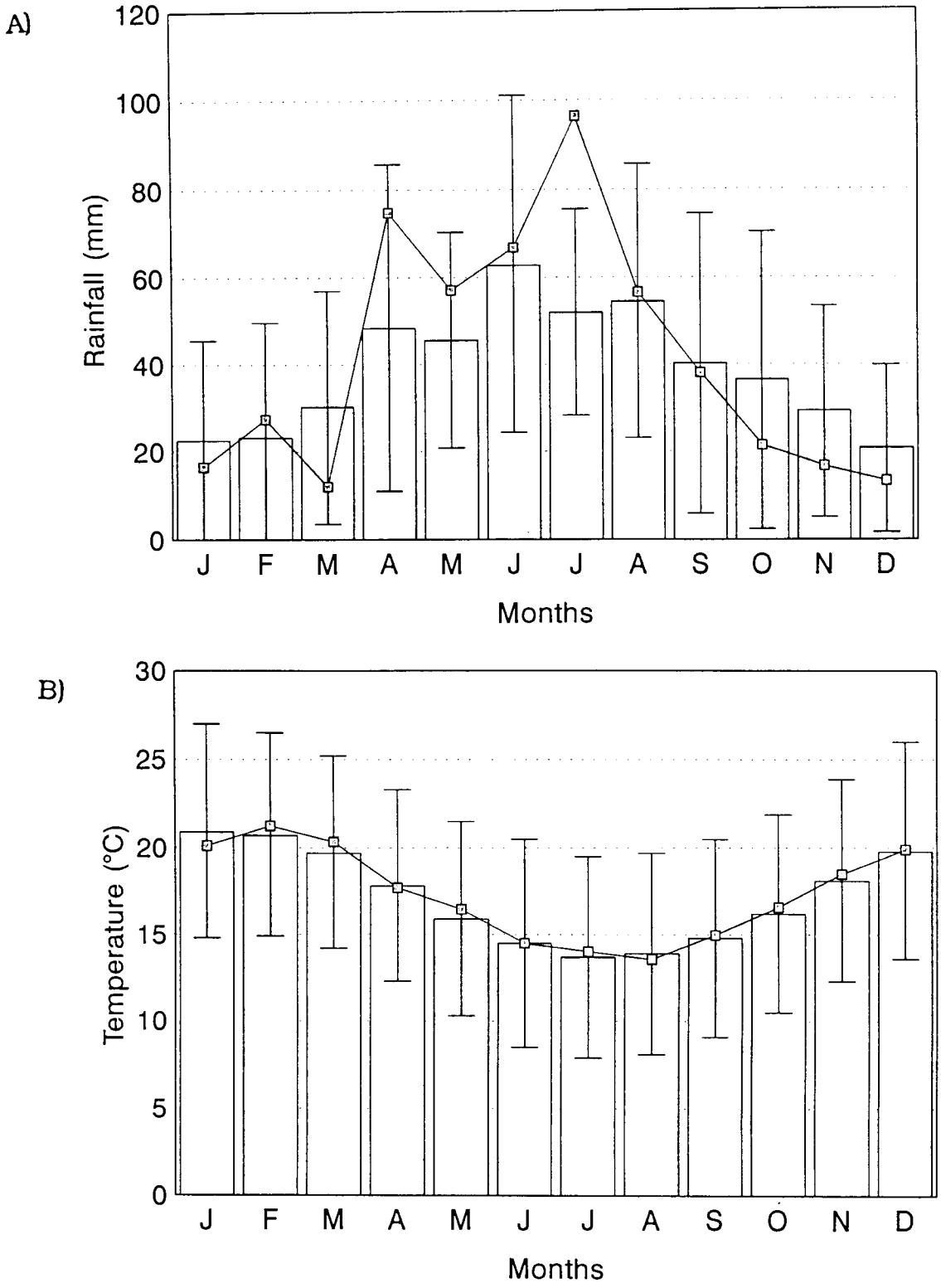
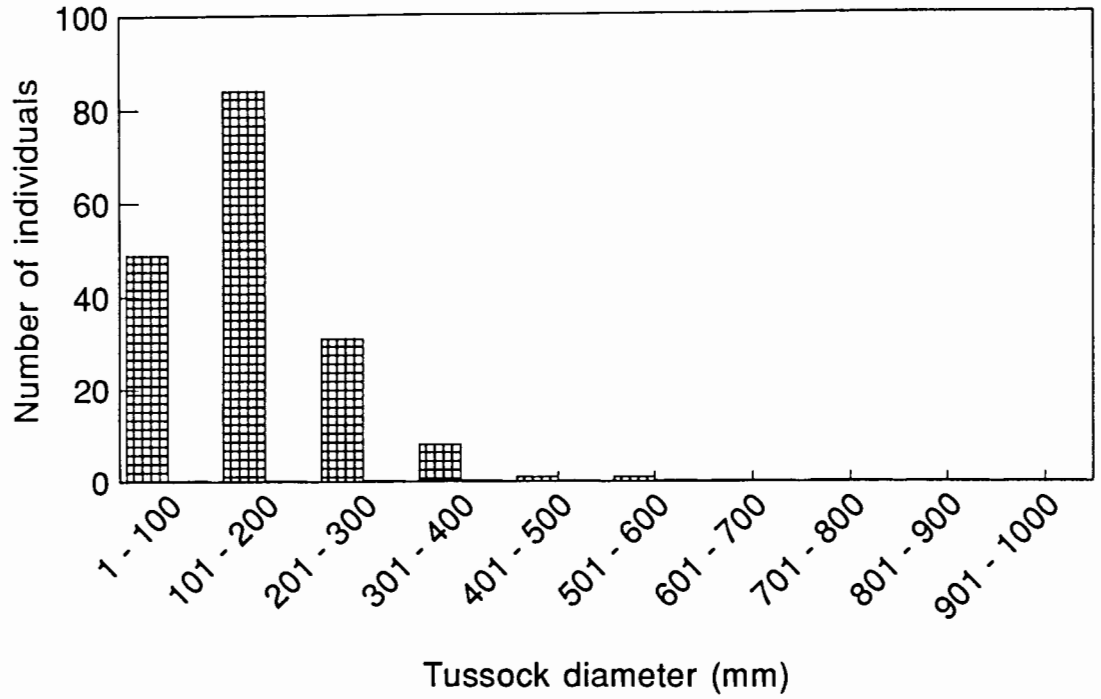


Figure 3.2. Climate diagram for the study sites: Zoetendalsvallei and Zeekoeivlei (Agulhas Plain), and De Hoop and Elandspad (De Hoop Nature Reserve). Data are from the Cape Agulhas meteorological station (Weather Bureau).

A) Mean monthly rainfall (1894 to 1990) and for study period (from 1990 to 1993) at Cape Agulhas.

B) Mean monthly temperature in degrees Celsius (°C) (from 1961 to 1990) and for the study period (from 1990 to 1993) at Cape Agulhas.

a) *T. insignis*



b) *T. erectus.*

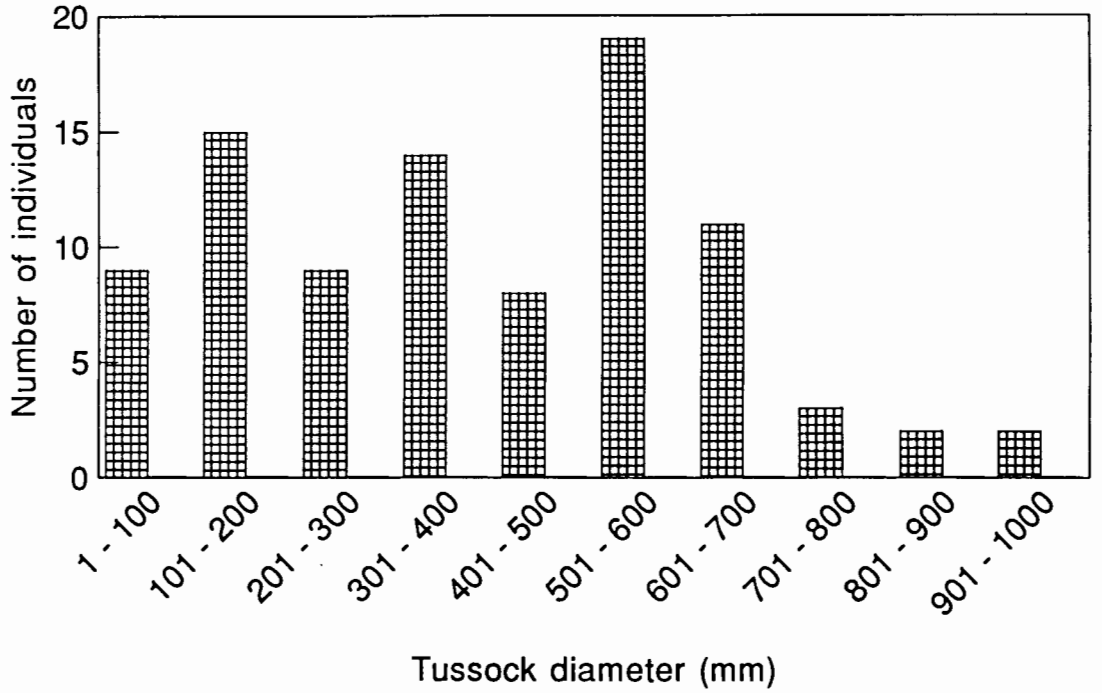
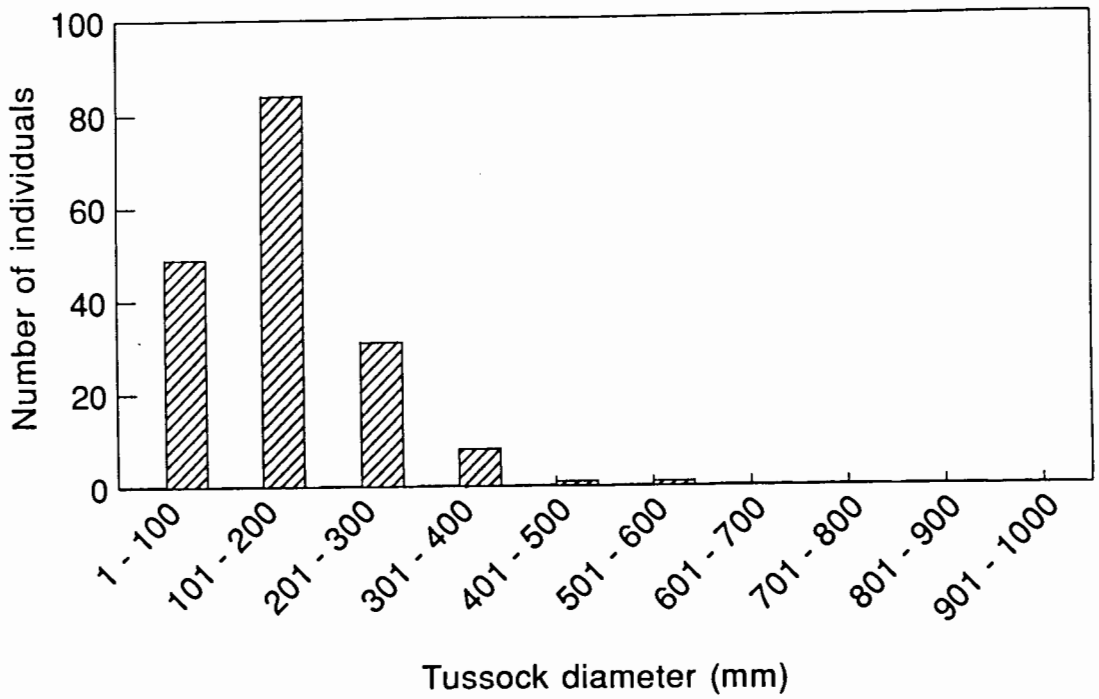


Figure 3.3. Distribution of a) *T. insignis* and b) *T. erectus* burnt ▦ adult plants in plant tussock diameter (mm) categories. Data are of total number of individuals in 60 1 X 1 m quadrats. *T. insignis* data were collected 34 months after a late summer burn and *T. erectus* data were collected 20 months after a summer burn, at De Hoop Nature Reserve in the southern Cape.

a) *T. insignis*



b) *T. erectus*

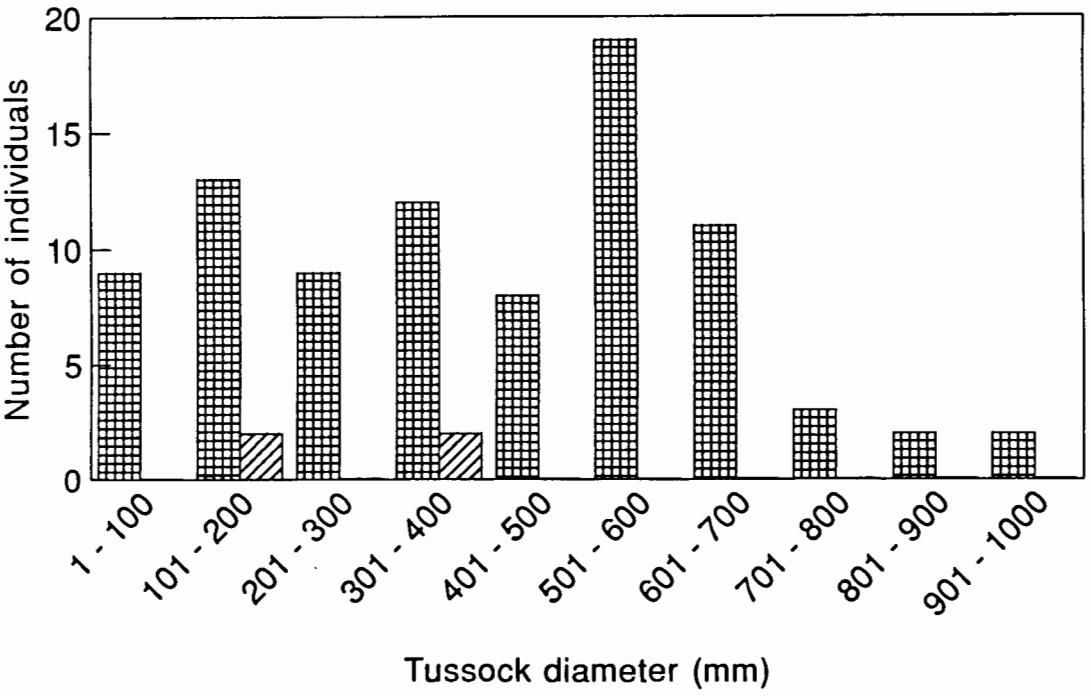


Figure 3.4. Distribution of a) *T. insignis* and b) *T. erectus* dead ▨ and live ▦ adult plants in plant tussock diameter (mm) categories. Data are total number of individuals in 60 1 X 1 m quadrats. *T. insignis* data were collected 34 months after a summer burn and *T. erectus* data were collected 20 months after a late summer burn, at De Hoop Nature Reserve in the southern Cape.

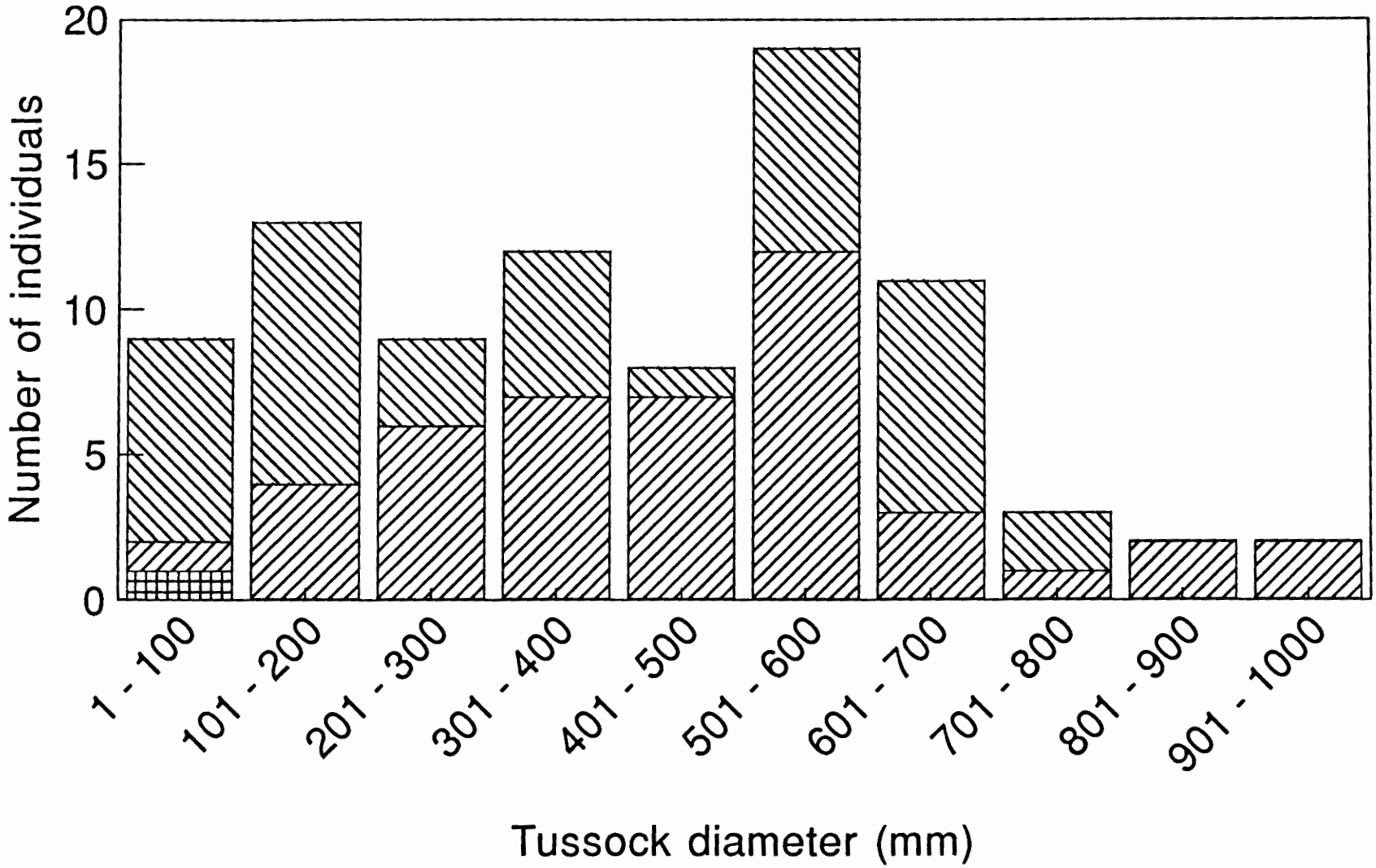


Figure 3.5. Distribution of *T. erectus* resprouting adult plants with different patterns of vegetative regrowth (i.e. resprouting from the middle of the tussock only ▦ from the edge of the tussock only ▨ and from all over the tussock ▧) in plant tussock diameter (mm) categories. Data are total number of individuals in 60 1 X 1 m quadrats. Data were collected 20 months after a late summer burn, at De Hoop Nature Reserve in the southern Cape.

Table 3.2. Estimates of the number of *T. erectus* resprouting culms after fire. Data are total number of culms recorded in 60 1 X 1 m quadrats and mean number of culms per plant (n = 88) in the total, reproductive (i.e. bears an inflorescence), unreproductive unbranched and unreproductive branched categories. Proportions (%) of culms with respect to total numbers of culms recorded in each category are displayed. Data were collected 20 months after a late summer burn, at De Hoop Nature Reserve in the southern Cape.

Culm type	Total	%	Mean	S.D.
Total	7078	100.00	80.43	90.87
Reproductive	851	12.02	9.67	35.53
Unreproductive - branched	921	13.01	10.47	19.57
Unreproductive - unbranched	5306	74.97	60.30	60.32

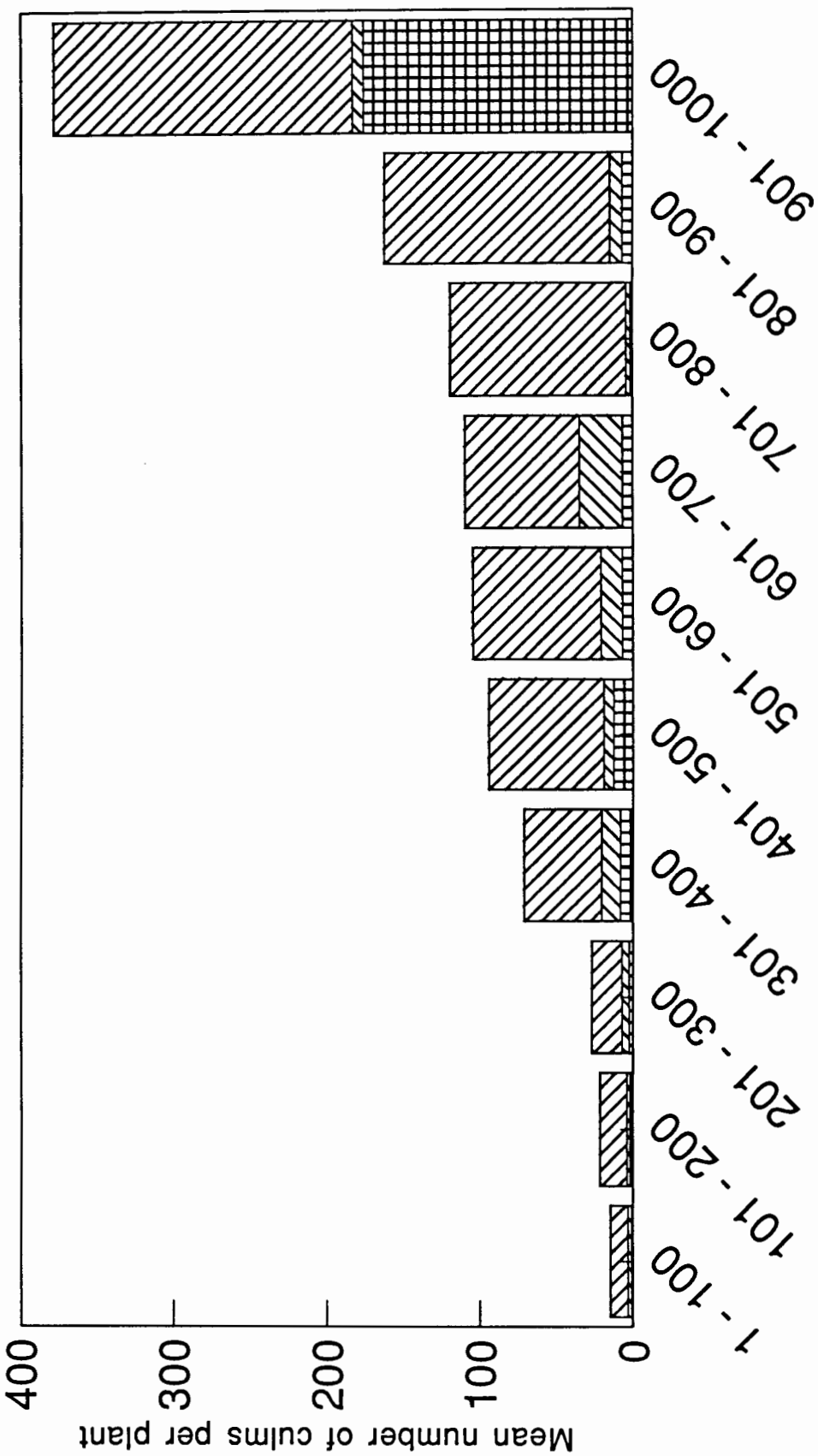


Figure 3.6. Mean number of *T. erectus* culms per plant (n = 88) in the reproductive (i.e. bears an inflorescence) , unreproductive unbranched and unreproductive branched categories, in relation to tussock diameter. Data were collected 20 months after a late summer burn, at De Hoop Nature Reserve in the southern Cape.

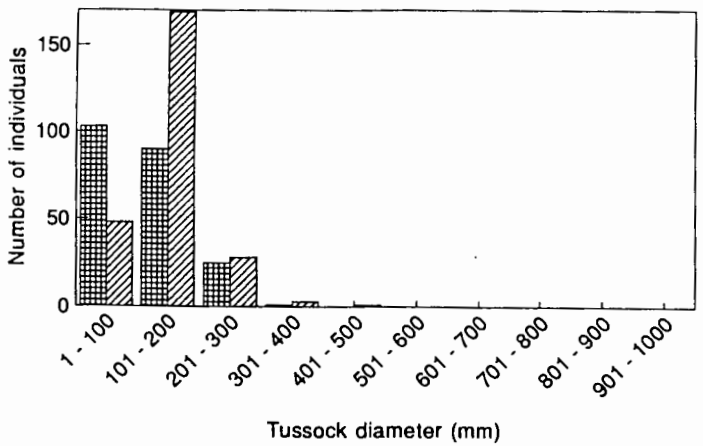
Table 3.3. Spatial heterogeneity of *T. insignis* and *T. erectus* adults plants and seedlings after fire and harvesting, as measured by variance to mean ratios. Data were collected in 60 1 X 1 m randomly placed quadrats at one recording period (December 1993) 34 months after a summer fire for *T. insignis* and 20 months after a late summer fire for *T. erectus*, at De Hoop Nature Reserve in the southern Cape. Data were collected in 100 1 X 1 m randomly placed quadrats at two recording periods (i.e. the first (1993) and second (1994) flowering season) after harvesting at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

Species	Spatial heterogeneity		
	Adults	Dead adults	Seedlings
After fire			
T. insignis	*	1.17	6.76
T. erectus	1.04	0.95	0.98
After harvesting			
T. insignis 1993	2.34	1.19	1.74
1994	2.13	1.45	0.25
T. erectus 1993	1.90	1.65	1.00
1994	1.11	1.00	3.58

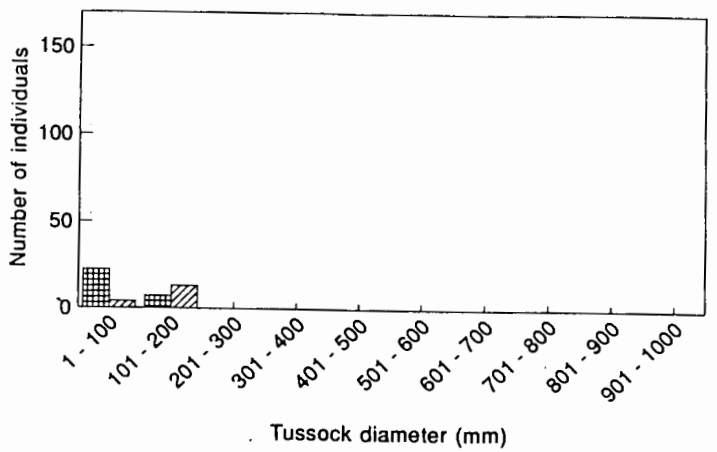
* no variance to mean ratios can be calculated on these data due to zero mean and variance values.

a) *T. insignis*

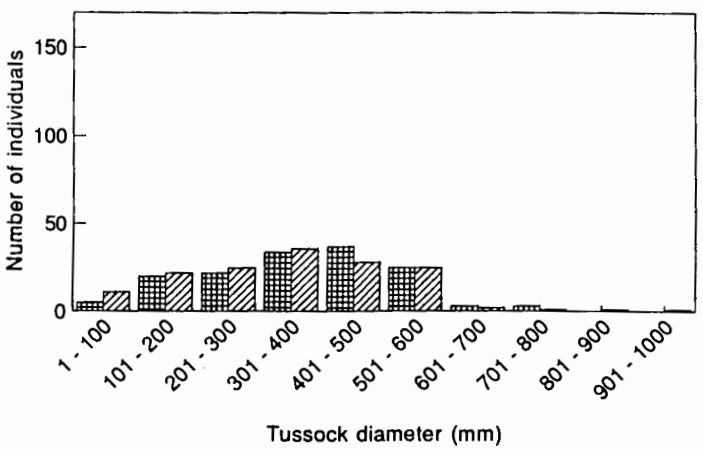
i) Harvested vegetation



ii) Unharvested vegetation



b) *T. erectus*



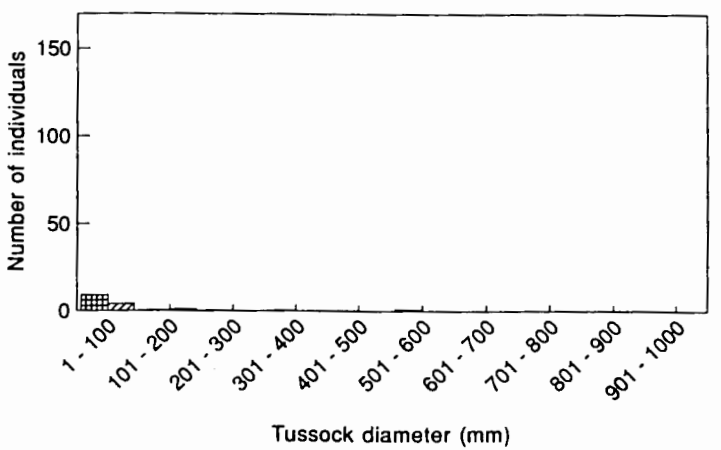
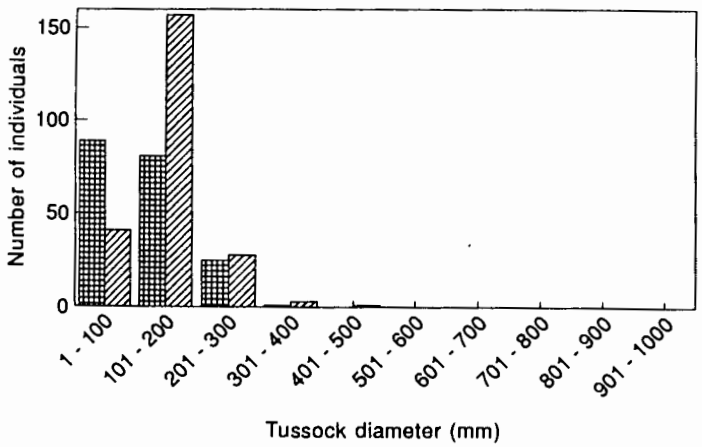


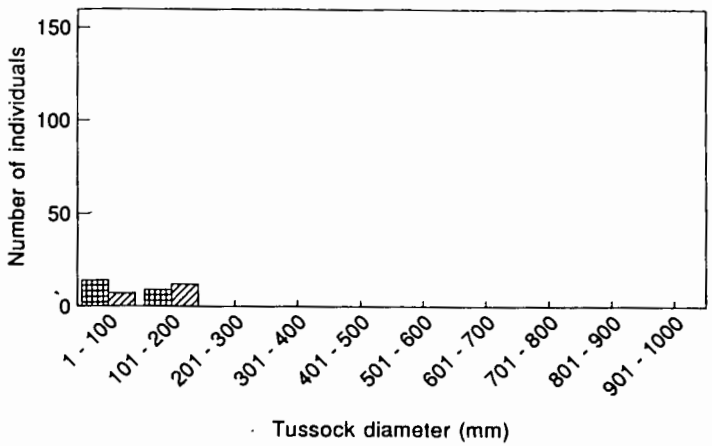
Figure 3.7. Distribution of a) *T. insignis* and b) *T. erectus* harvested and unharvested adult plants in plant tussock diameter (mm) categories. Data are total number of individuals in 100 1 X 1 m quadrats. Data were collected in the first (1993) ▦ and second flowering season after harvesting (1994) ▨ , at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

a) *T. insignis*

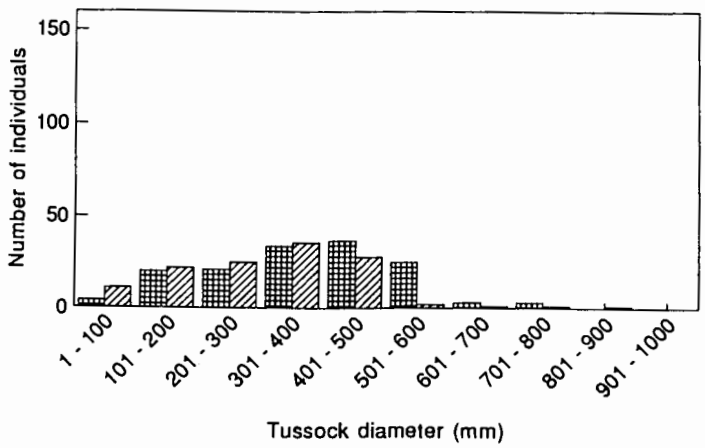
i) Living



ii) Dead



b) *T. erectus*



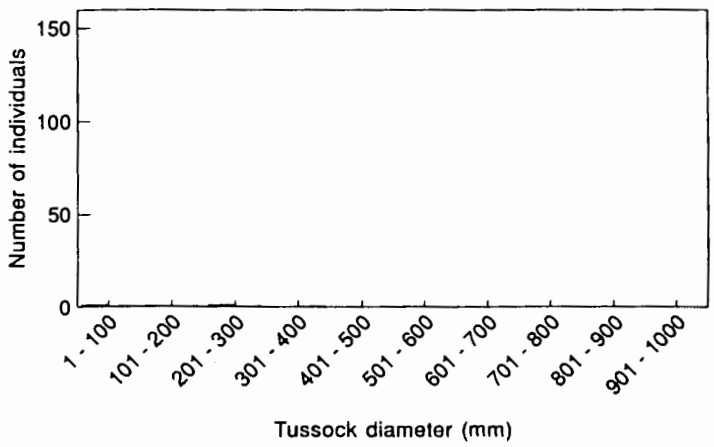


Figure 3.8. Distribution of a) *T. insignis* and b) *T. erectus* dead and live adult plants in plant tussock diameter (mm) categories. Data are total number of individuals in 100 1 X 1 m quadrats. Data were collected in the first (1993) ▦ and second flowering season after harvesting (1994) ▨ , at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

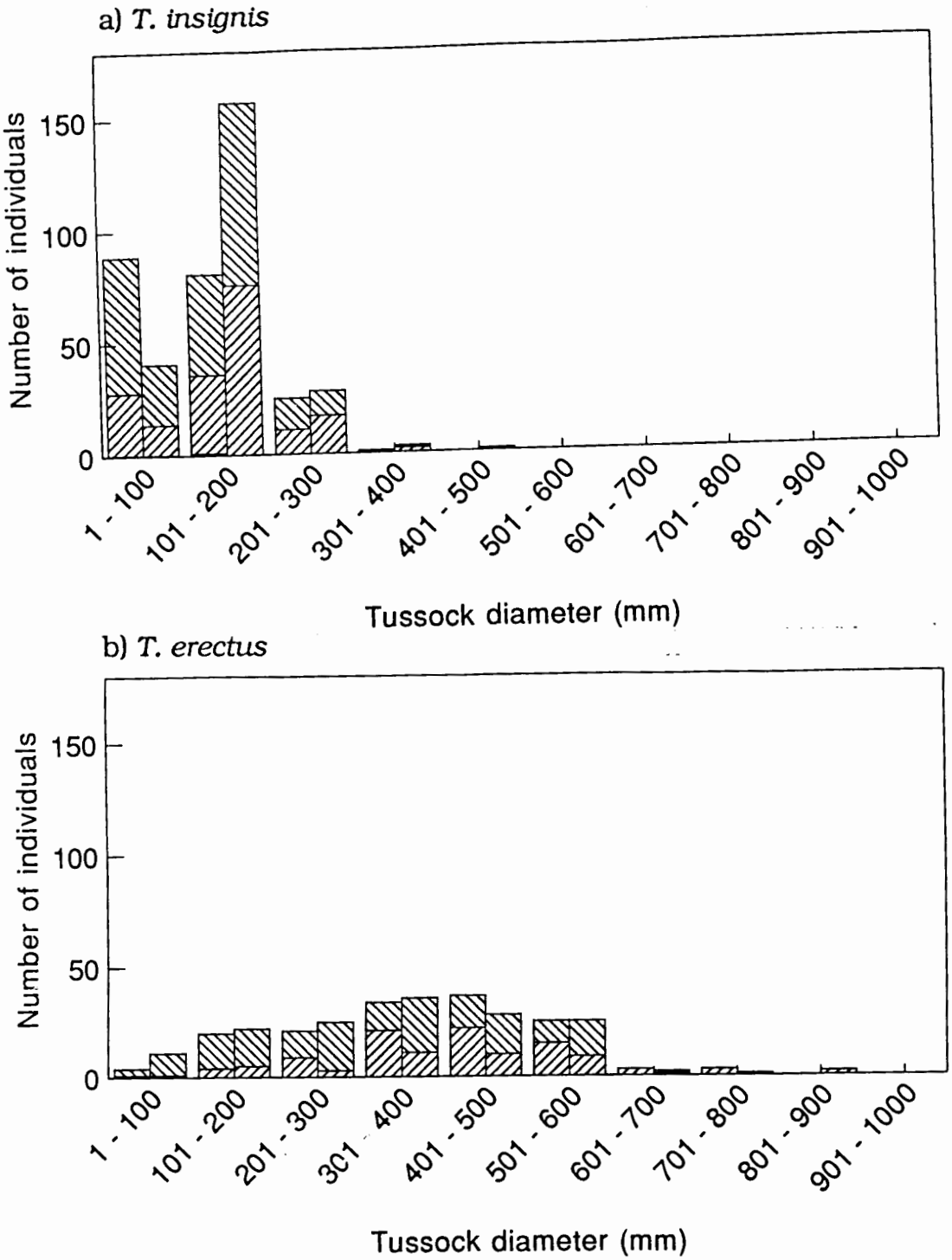


Figure 3.9. Distribution of a) *T. insignis* and b) *T. erectus* resprouting adult plants with different patterns of vegetative regrowth (i.e. resprouting from the middle of the tussock only ▦ , from the edge of the tussock only ▨ and from all over the tussock ▧) in plant tussock diameter (mm) categories. Data are total number of individuals in 100 1 X 1 m quadrats. Data were collected in the first (1993) and second flowering season after harvesting (1994), at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). At each data point the first bar represents the values for 1993 and the second bar represents the values for 1994.

Table 3.4. Estimates of the number of resprouting culms for *T. insignis* and *T. erectus* after harvesting. Data are total number of culms recorded in all plants (*T. insignis*: 1993 = 196, 1994 = 230; *T. erectus*: 1993 = 147, 1994 = 152) and mean number of culms per plant (*T. insignis*: 1993 n = 196, 1994 n = 230; *T. erectus*: 1993 n = 147, 1994 n = 152) in the total, reproductive (i.e. bears an inflorescence), unreproductive unbranched and unreproductive branched categories, in 100 1 X 1 m quadrats. Proportions (%) of culms with respect to total numbers of culms recorded in each category are displayed. Data were collected in the first (1993) and second flowering season after harvesting (1994), at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

Species	Year								
	1993				1994				Significance
	Total	%	Mean	S.D.	Total	%	Mean	S.D.	within species
T. insignis									
Total	3165	100.00	14.07	19.76	9389	100.00	38.17	30.78	* * *
Reproductive	437	13.81	1.94	4.25	3395	36.16	13.80	17.84	* * *
Unreproductive - branched	225	7.11	1.00	4.55	557	5.93	2.26	4.14	* *
Unreproductive - unbranched	2503	78.08	11.12	15.96	5437	57.91	22.10	19.71	* * *
T. erectus									
Total	10682	100.00	68.04	56.67	10187	100.00	64.89	47.47	N.S.
Reproductive	59	0.55	0.38	1.18	43	0.42	0.27	1.25	N.S.
Unreproductive - branched	5851	54.78	37.27	36.06	5047	49.54	32.15	27.80	N.S.
Unreproductive - unbranched	4772	44.67	30.39	31.00	5097	50.04	32.46	27.33	N.S.

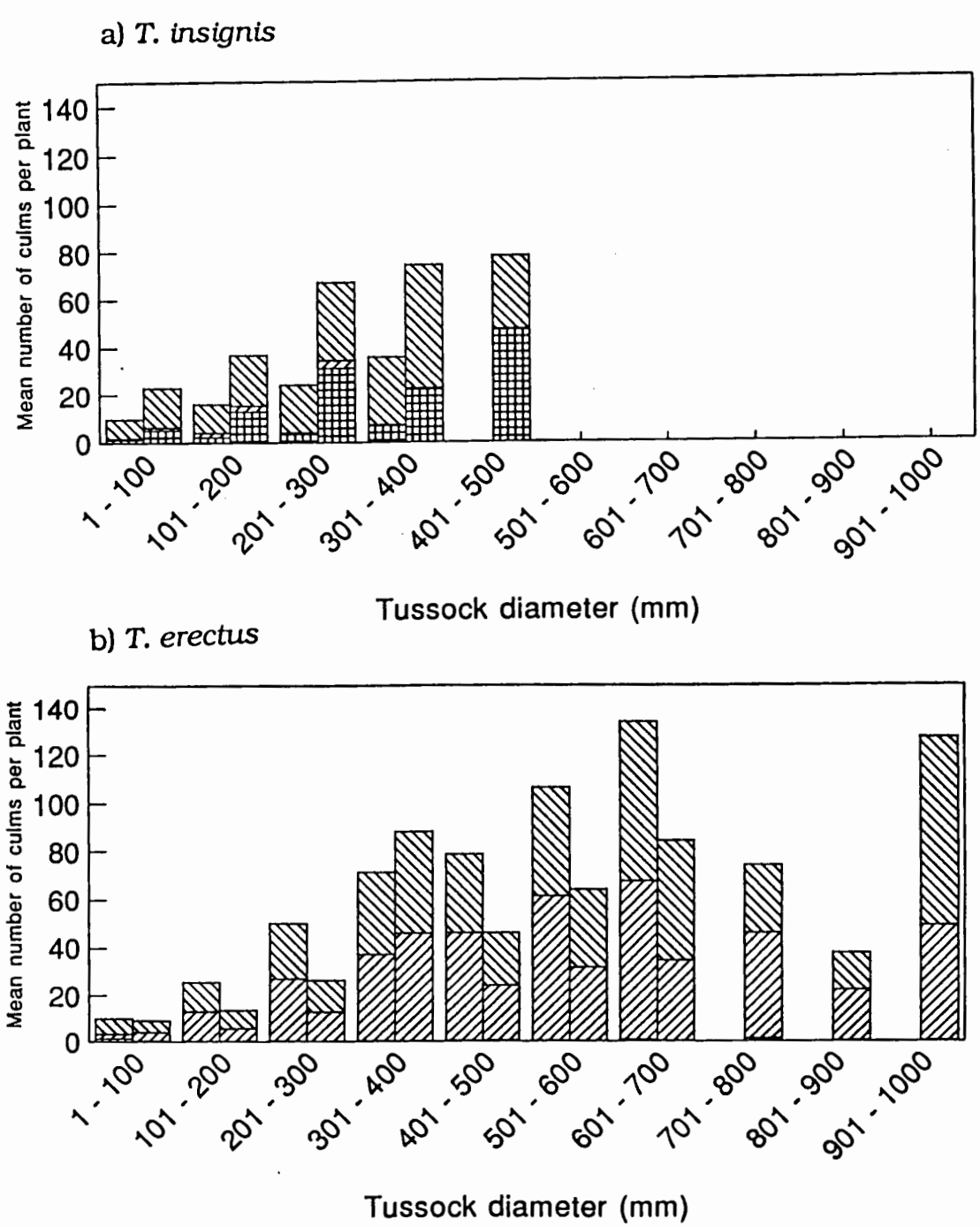


Figure 3.10. Mean number of a) *T. insignis)* (1993: n = 196, 1994: n = 230) and b) *T. erectus* (1993: n = 147, 1994: n = 152) culms per plant in the reproductive (i.e. bears an inflorescence) ▦ unreproductive unbranched ▨ and unreproductive branched ▨ categories. Data were collected in the first (1993) and second flowering season after harvesting (1994), at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). At each data point the first bar represents the values for 1993 and the second bar represents the values for 1994.

Table 3.5. Variation within and between *T. insignis* and *T. erectus* adult plant height after harvesting. Data are average (mean ± standard deviation) plant height (ground level to the tallest reproductive culm) (m) (*T. insignis*: 1993 n = 196, 1994 n = 230; *T. erectus*: 1993 n = 147, 1994 n = 152). Data were collected in the first (1993) and second flowering season after harvesting (1994), at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain). Two sample t-tests were used to test within and between species significance. * * * = $P < 0.001$, N.S. = non-significant.

	Year				
	1993		1994		
	Mean	S.D.	Mean	S.D.	Significance within species
T. insignis	59.45	33.50	64.58	19.81	N.S.
T. erectus	95.41	23.62	96.00	24.95	N.S.
Significance between species	* * *		* * *		

3.6 DISCUSSION

Plant mortality after disturbance

No plants of both species escaped from being burnt. This is possibly due to the fact that both species grow in sandy valley slacks with no boulder clumps etc. that could act as refuges for *Thamnochortus* plants. In contrast, a few plants of both species escaped harvesting. The greater number of *T. insignis* plants escaping harvesting compared to *T. erectus* is possibly due to there being more small shrubs at the *T. insignis* site acting as refuges for *Thamnochortus* plants. Fire is an unselective disturbance type, whereas harvesting is selective, with the majority of unharvested individuals of both species having a small tussock diameter. The practice of leaving a few unharvested plants ensures that there is seed input into the seed bank in the year following harvesting (Section 2.6). Moreover, many more adults and seedlings of both species survived harvesting compared to fire, suggesting that harvesting has less of an impact on population dynamics than fire. The uneven distribution of dead plants across the post-disturbance size classes can possibly be attributed to disturbance intensity. Intense fires burn away large amounts of above-ground biomass and produce a heating front in the soil and brushcutting results in mechanical damage, which is often sufficient to kill meristematic tissues in the tussock base (Rundel *et al.* 1987). Small plants with shallow tussock bases and less tussock base biomass are most sensitive to heat and mechanical damage. Large plants, however, may also be sensitive if they have been exposed by erosion or have built up large amounts of dead tissues which may ignite (Rundel *et al.* 1987).

Regeneration after disturbance

After fire, regeneration of the non-sprouter, *T. insignis*, is by the establishment of new individuals from seed (Bell et al. 1984, Keeley and Zedler 1978). Considering the large numbers of seedlings recruited after fire,

population replacement is ensured and population expansion is probable despite the expected high seedling mortality (Section 2.5.8, Rundel *et al.* 1987, Meney *et al.* 1994). After fire, regeneration of the resprouter, *T. erectus*, is by resprouting from subterranean buds and by the establishment of new individuals from seed. Considering the low numbers of seedlings recruited after fire, population expansion is not probable although population replacement is ensured (Section 2.5.8). Meney and co-workers (1994), however, found that all four resprouter and two non-sprouter species of Australian Restionaceae studied had the capacity to restore parent densities from germinants in the first year after fire, but high seedling mortality and no further recruitment resulted in less seedlings than replacements at the end of the third year after fire.

After harvesting, regeneration of both species was by resprouting and by the establishment of new individuals from seed. Considering the large numbers of *T. insignis* seedlings recruited after harvesting, population replacement is ensured and population expansion is probable despite the expected high seedling mortality (Section 2.5.8, Rundel *et al.* 1987). Despite the low numbers of *T. erectus* seedlings after harvesting, population replacement was expected as few adult plants died as a result of the disturbance.

Vegetative response

Underground organs of resprouters, such as *T. erectus*, often account for a considerable portion of the plant biomass (Section 5.3) and act as storage organs for nutrients and carbohydrates (Pate *et al.* 1990, 1991; Bowen and Pate 1993). The non-sprouter, *T. insignis*, also has a considerable portion of the plant biomass devoted to underground organs (Section 5.3). Large temperature elevations during burning, occur only in the upper few centimeters of soil, thus, underground buds may escape fire damage. A more intense fire may have resulted in greater plant mortality, due to the death of these perenneating organs (Gill 1981b).

Disturbance stimulates sexual and asexual reproduction in many plants. The years immediately following disturbance typically have the highest above-ground biomass accumulation rates in shrubland ecosystems and these rates depend on reproductive mode (Christensen 1985). Non-sprouters have a slower rate of vegetation recovery than resprouters, as this would be determined largely by the rate of breakdown in seed dormancy after fire and possibly by the rate of importation of seeds from adjacent unburnt areas. This was evident in both the fire and in the harvesting study, although the differences were not great after harvesting. The rate of initial recovery is dependent on the amount of below-ground translocatable resources and presence of dormant buds and, thus, the response can be variable. Harvesting below the critical height would result in damage to the growing culm tips and result in failure to resprout (Griffin and Hopkins 1981, Parisi 1985). Culm regrowth for both species was independent of plant size and was from the edge and/or all over the tussock. The observation that *T. erectus* resprouted mainly from the edge of the tussock and rarely from the middle of the tussock, suggests that the majority of buds were situated on the periphery of the tussock. Plants require a minimum level of vegetative production before starting the reproductive processes (Hillman 1962). The speed with which this initial level is reached depends on the growth pattern and life history of the species. Both study species are evergreen, which usually have high growth and maintenance costs (Merino 1987), and this could potentially result in delayed regrowth. Biomass accumulation rates will also decrease with time due to self imposed stress caused by the accumulation of old or dead tissue (Hilbert *et al.* 1981), the increase in plant biomass, and the resource requirements in relation to the constant amount of available resources. Recovery to pre-fire above-ground biomass levels in heathlands and mediterranean shrublands occurs in 7-20 years (e.g. Kruger 1977, van Wilgen 1982), although this may depend on site conditions such as moisture availability which are unrelated to fire. Both study species showed great resilience to disturbance, and vegetative recovery was rapid, especially after harvesting (see Parisi 1985 for similar findings for a *Thamnochortus* species). It is predicted that recovery to pre-fire above-

ground biomass levels would occur in 5-7 years for *T. erectus* and 8-10 years for *T. insignis*. The predicted recovery to pre-harvesting above-ground biomass levels would be shorter, namely in 3-5 years for both species. Although flowering is not stimulated by disturbance, both *T. insignis* and *T. erectus* produced inflorescences in the year following harvesting. The non-sprouter had greater numbers of reproductive culms than the resprouter. *Thamnochortus erectus* also produced inflorescences in the year following fire, although only individuals in the largest size class produced large numbers of reproductive culms. Reasons for this observation could be that larger plants have greater concentrations of stored carbohydrates than smaller plants (Rundel *et al.* 1987, Malanson and Trabaud 1988), or that larger plants have a greater functional absorptive surface of the root than small plants and thus maintain higher water potentials following fire, or that larger plants have greater concentrations of stored nutrients, such as nitrogen, or increased uptake rates following disturbance than smaller plants, or that, in relative terms, the cost of producing the same amount of new growth would be greater for smaller than for larger plants (Moreno and Oechal 1993). The presence of large individuals, at the time of the fire, that contribute to the seed bank in the year after fire are, however, not critical for the resprouter as regeneration is not dependent on soil-stored seed after fire.

For species that are able to establish seedlings at any time during the post-disturbance period, there is no advantage to maximize reproductive effort before the disturbance is expected to occur. There may, however, be an advantage to flowering early after disturbance because seedling establishment and survival may be more enhanced in the less competitive early post-disturbance environment (Ostertag and Menges 1994). An early peak in reproductive effort may be advantageous because plants may have more resources to allocate to flowering in the early post-disturbance years. Fynbos communities can return to pre-burn covers rapidly and if the fire-return interval is unpredictable an early flowering peak will minimize the chances of frequent fires eliminating or drastically reducing the population.

Unpredictable fire-return intervals and early post-fire reproduction have been found to be important in other periodically burned ecosystems (Ostertag and Menges 1994, Zedler and Zammit 1989).

The ability of vegetation to survive disturbance and the availability of seed is dependent on the season of harvest. Plants are least susceptible to disturbance during periods of dormancy due to the availability of resources for regrowth. Reduction in plant above-ground biomass during growth periods (*T. insignis*: June to July, *T. erectus*: April to May) would result in slow plant recovery, and higher levels of plant mortality, especially in smaller individuals which have a reduced buffering capacity (Rundel *et al.* 1987). Vegetation age could also effect the potential to recover after disturbance. Further studies are needed to test whether the two study species show different patterns of recovery after disturbance in different seasons or with differently aged vegetation.

Seedling recruitment

For both species, the seed source for recruitment after disturbance could either be persistent seed in the soil seed bank or immigration of seed from nearby undisturbed vegetation (Willson 1983, Grubb 1987). Although immigration of seed cannot be excluded, evidence including similar seedling densities near to and far from undisturbed vegetation and the large distance separating undisturbed and disturbed vegetation (pers. obs.) does not seem to support this suggestion.

Fynbos non-sprouters rely mainly on onsite-stored seed for germination and recovery (e.g. Kruger and Bigalke 1984). *Thamnochortus insignis* recruitment after fire depends on seeds produced over several seasons to ensure good regeneration. Despite steady seed losses, *T. insignis* has a large seasonally persistent seed bank (Section 2.5.6, 2.5.7 and 2.6). At the time of the fire, the seed bank would have been comprised of seed from seasons since the last fire and up to the 1990 reproductive season. Given that the fire

happened at the seed maturation stage, it is unlikely that the mature seed in the inflorescences at the time of the fire survived and contributed to seedling recruitment. Despite this, *T. insignis* probably had more seeds in the soil seed bank before the disturbance event, by several orders of magnitude, than seedlings after the disturbance event (see Keeley 1977).

A intense fire may result in plant mortality of the resprouter, *T. erectus*, due to the death of the perenneating organs (Gill 1981b). In these circumstances population survival would depend on the large seasonally persistent seed bank (Section 2.5.6, 2.5.7 and 2.6). A persistent seed bank would also ensure population survival after fire in any season, as is also the case for *T. insignis*. At the time of the fire, the seed bank would have comprised of seed from seasons since the last fire and up to the 1991 reproductive season. As the majority of adult plants were resprouting, recruitment did not depend on seeds produced over several seasons to ensure good regeneration, and an average seed production event in the year preceding fire would have ensured sufficient seed to ensure replacement of dead parent plants. *Thamnochortus erectus* probably had more seeds in the soil before the disturbance event, by several orders of magnitude, than seedlings after the disturbance event (see Keeley 1977).

Many but not all seeds of both species were destroyed by the fire, by direct combustion or from lethal heating (pers. obs., see Meney *et al.* 1994). An assessment of the germinability of residual seeds is needed to determine whether complete depletion of the seed bank had occurred after the fire and whether residual seed are able to contribute to the seed bank. Meney and co-workers (1994) found that the seed banks of five dominant Australian Restionaceae species were completely depleted after fire. A high intensity burn would certainly result in the death of seeds in the litter layer, although many soil-stored seeds would survive (e.g. Purdie 1977) as heat transfer down the soil profile is quickly attenuated (Christensen 1985). Temperature increase in the soil is reduced by litter, although ignition of this layer could result in elevated temperatures over a longer period of time (Christensen

1985). Thus, litter left on the ground following harvesting may effect recruitment after fire through the change in fire characteristics that effect seed germination, as well as inter-fire seedling recruitment through the change in the physical environment and by smothering seedlings (Section 2.5.8). It is also unlikely that seeds buried deeply in the soil will experience the same dormancy breaking stimulus that seeds lying in the upper 1-2 cm of the soil's surface experience (Auld 1986). As a result, many viable soil-stored seeds do not contribute to seedling recruitment after fire.

The large increase in seed seedling density after disturbance for *T. insignis* suggests that direct and/or indirect disturbance related cues (especially fire-related), as well as alternating temperatures normally experienced in autumn are effective in maximizing the breaking of dormancy in the species. Examples of disturbance related cues are allelopathic effects (Pierce 1990), heat (Musil and De Witt 1991, Musil 1991), charate (Keeley and Pizzorno 1986), smoke (De Lange and Boucher 1990, Brown 1993a, 1993b, Brown *et al.* 1993, 1994), and indirect interactions such as changed environments (Naveh 1975, Gill and Groves 1981, Rundel 1981, Kruger 1983, Parker and Kelly 1989, Keeley 1991, Bell *et al.* 1993), increased oxygen concentrations, increased light, changes in the spectral composition, increased fluctuations in soil temperature (Appendix B) or cold conditions in the post-disturbance environment (e.g. Deall and Brown 1981, Mitchell *et al.* 1986, Brits 1986, Pierce 1990, Kilian 1991). These traits are not isolated and many cues may act on the same species to break seed dormancy (Keeley *et al.* 1985). The observations that *T. insignis* seedlings in the post-fire vegetation were multi-aged and that seedling recruitment occurs in inter-fire years in both harvested and unharvested vegetation (Section 2.5.8, Singleton 1991), suggests that disturbance-related effects are not the only factors which cue germination response in the species. Another explanation of the observed massive seedling recruitment after disturbance, could be immigration of wind-borne seed into post-disturbance vegetation which germinates when favorable conditions prevail or the existence of polymorphic seeds (i.e. seed having simple germination requirement and another seed type having a

complex germination requirement) in the seed bank. A more probable explanation is that the species produces one type of seed with a simple germination cue (e.g. increased soil temperature fluctuations), which ensures that the species establish in mature vegetation in canopy gaps and in post-disturbance vegetation. Removal of the above-ground biomass during disturbance would increase soil temperature fluctuations especially during autumn (Appendix B), resulting in an increased germination response (Thompson *et al.* 1977, Brits 1986, Brits and Brown 1991, Brown *et al.* 1994, Pierce and Moll 1994). Removal of vegetation could also reduce the possibility of fungal pathogen attack of seeds or seedlings (Augspurger 1984) or favorably change the light quality (Solangaarachchi and Harper 1987). Singleton (1991) showed that no *T. insignis* seeds germinated in a temperature regime simulating summer conditions (30°C/15°C; 10/14 hour light and dark conditions) compared to approximately 6% cumulative germination, for seeds germinated in a temperature regime simulating winter/early spring conditions (20°C/10°C; 10/14 hour alternating light and dark conditions). A staggered seedling recruitment pattern allows plants to average their reproductive success over time, reducing both opportunity and risks. The value as a survival mechanism is clear, particularly where post-disturbance climatic conditions vary depending on the season in which the fire occurs. Efficient *T. insignis* seed dispersal is also important in ensuring a spatially extensive post-disturbance recolonization, and may permit escape from unfavorable conditions in time and space.

The observation that low number of *T. erectus* seedlings recruited after disturbance, suggested that disturbance related cues do not maximize germination in the species. The results from the seedling emergence studies and the observation of germination in the field, suggests that germination of *T. erectus* seed is cued by early winter soil temperature and moisture conditions (Section 2.4.6.3 and 2.5.8).

Post-fire *T. insignis* and post-harvesting *T. insignis* and *T. erectus* seedling distributions were highly clumped which could either be due to a clumped

pre-fire distribution of seed in the seed bank and/or variable seedling recruitment and survival. Reports of clumped post-fire seedling distributions for perennials are common, with the most highly clumped distributions being found among non-sprouters (e.g. Rundel *et al.* 1987, Musil and de Witt 1990). These clumped distributions have been related to the creation of environmental heterogeneity affecting seedling recruitment (e.g. litter), seed accumulation in and increased germination and seedling survival in "safe sites" such as shallow depressions on the soil surface which experience higher moisture levels, seed accumulation at barriers to air flow such burnt remnants of plants, non-random heating effects resulting from microscale differences in fire intensity and duration in burning (e.g. Davis *et al.* 1989), redistribution of pre-disturbance seed assemblages, exogenous seed input, variation in soil water repellency affecting germination (Osborn *et al.* 1967), selective herbivory and competition or allelopathic inhibition of seed germination either by residual plants or seedlings of fynbos species. Thus, species' distributions and abundances after a disturbance event could reflect a complex set of interactions between pre-disturbance seed assemblages, pre-burn fuel distribution and other influences on fire behaviour, post-disturbance seed dispersal and post-disturbance mortality factors. The concentration of recruitment of *T. insignis* in the post-fire environment makes patterns occurring then especially important in the population biology of the species.

Limitations and remaining questions

A major weakness of this study was that it was conducted at one study site for each species and for each disturbance type, and that it included only one disturbance event. In comparative studies, an increase in the number of study sites is prohibitive in terms of financial costs and time, although it would have increased the generality of the results. Seedling density following fire is characteristically variable because of localized differences in wind, fuel, temperature, and moisture (Keeley and Keeley 1981). The number of seedlings per pre-burn individual is also variable between

disturbance events, due to factors such as pre-disturbance adult plant densities, season of the disturbance and post-disturbance climatic conditions (Bond *et al.* 1984, Parker 1987). It is possible that higher levels of seedling recruitment for *T. insignis* is possible after a late autumn burn, as this would occur after seed dispersal and incorporation into the seed bank, and follow up rains would be probable. Data should have ideally been collected at frequent intervals following the disturbance event. As data were collected at one period after fire only, seedling estimates could be the result of environmental influence on seedling survival and not necessarily germination and seedling establishment. Fire is known to remove or reduce the effects of factors such as pathogens, nutrient limitations and seedling predators, which exert a negative influence on seedling survival in unburnt vegetation (Christensen and Muller 1975, Van Wilgen and Le Maitre 1981, Brown and Mitchell 1986, Stock and Lewis 1986, Musil and Midgley 1990). For these reasons, detailed germination studies need to be conducted on both species to elucidate the exact mechanisms of seed dormancy breaking in *T. insignis* and *T. erectus*. There is in particular a need to investigate Restionaceae fire-related germination cues and to related these to the fire response strategies of the individual species. Generally, however, it was felt that trends were obvious and conclusions reached were well founded.

In summary, this study provides evidence that a single disturbance event increases the successful establishment of the non-sprouter, *T. insignis*, largely by massive seedling recruitment. In contrast, a single disturbance event does not increase the successful establishment of the resprouter, *T. erectus*, and populations maintain themselves by vegetative growth. Both species are able to resprout and resume seed production rapidly after harvesting. *Thamnochortus insignis* can be seen as a pioneer species and *T. erectus* can be seen as persistent species.

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CHAPTER 4

GENERAL CONCLUSIONS

4.1 PREAMBLE

This chapter highlights the major findings of this study as well as the limitations. Suggestions for future research and solutions to the problems encountered during the course of the project are also proposed. The aims of this study were:

1) To investigate and compare the effect of harvesting on the seed biology, especially the soil seed banks of two thatching reed species, namely *Thamnochortus insignis* and *Thamnochortus erectus*.

2) To investigate mortality, vegetative regrowth and seedling recruitment of the two species after fire and harvesting.

3) To provide comparative insights into the biology of the two species each of which have different life history modes.

4) To provide guidelines for sustainable harvesting, based on sound ecological principles and an understanding of the biology, response to disturbance, and life history modes of the two species.

In general, very little is known about Restionaceae population dynamics and population processes that depend on the distribution and behaviour of seeds (Leck et al. 1989). The primary contribution of this study is that it is the first comprehensive study on the seed and seedling biology of African Restionaceae. A feature of this study is that many components of the life cycles of two allopatric and closely related species were studied, and similarities and differences between the two species were investigated. It was particularly useful to have physiognomically similar species each with a different regeneration mode for comparison, as this highlighted the distinctive features of each species. A major strength of the study was that it focused on limited spatial as well as limited temporal heterogeneity, as field research was conducted over a two year period. The approach of using a number of methods to study a range of characteristics of the species, and often a number of methods to study a single characteristic, proved extremely effective. This is one of the few experimental studies in which both the inputs and losses to the seed bank were quantified (Cavers 1983,

Fenner 1987, Leck *et al.* 1989). The "seed budget" approach (Mallik *et al.* 1984, Andersen 1989) was found to be extremely useful to integrate the important processes influencing seed bank dynamics. This study highlights the strengths of using generalised linear models (GLIM) (McCullagh and Nelder 1983) for interpreting seed bank data, which has previously been problematic to analyze. The information collected revealed many interesting patterns in the adaptations of the species to their disturbance-prone environment.

The major findings are discussed in relation to the studies' objectives.

4.2 MAJOR FINDINGS

4.2.1 REPRODUCTIVE BIOLOGY

Soil seed bank densities of both species were high; with that of the non-sprouter, *T. insignis*, being approximately 2 times larger than that of the resprouter, *T. erectus*. This was attributed to greater seed production in *T. insignis* compared to *T. erectus*, rather than to longer survival of seed in the soil. Both species produced considerably more seeds than were incorporated into the seed bank and it was during this life history stage that the largest seed losses were observed for both species. The seed bank densities of both species were distinctly seasonal, with direct seed counts for *T. insignis* varying between 1633 ± 2601 (mean ± standard deviation) seeds per m^2 before dispersal and 3773 ± 6027 seeds per m^2 after dispersal. Seed counts for *T. erectus* varied between 1134 ± 2644 seeds per m^2 before dispersal and 2530 ± 3482 seeds per m^2 after dispersal. Seed bank estimates from germination were lower for both species. Annual seed production and seed bank densities of both species showed large annual variations, as well as variations between species. Harvesting resulted in a drastic decline in both seed production and post-dispersal seed bank density for both species. Active dispersal of seed during harvesting resulted in an increase in pre-dispersal seed bank density for both species. Both species had seasonally

persistent seed banks, and seed losses over the year following seed input were moderate. An accumulation of seeds in the soil over the two years was observed for both species. Seed burial showed that seed persistence and losses in seed banks differed between species and experimental seed bank type. *Thamnochortus erectus* showed greater seed persistence and *T. insignis* showed greater seed losses. These results conflict with actual observations of seed bank densities. Burial boxes showed greater seed persistence and burial bags showed greater seed losses for both species. Inter-fire recruitment of both species was limited in mature vegetation, although that of *T. insignis* was approximately 11 times greater and more variable than for *T. erectus*. The "open" microhabitat was favoured by seedlings of both species. Seedling survival, especially for *T. insignis* was low with very few seedlings surviving for longer than a year.

4.2.2 RESPONSE TO DISTURBANCE

No plants of either species escaped from being burnt. In contrast, a few plants of both species escaped harvesting. Fire is an unselective disturbance type, whereas harvesting is generally selective, with small *T. erectus* individuals being harvested.

Fire resulted in greater adult plant mortality for both species than harvesting. The decrease in pre- to post-disturbance adult plant density for both species varied according to disturbance type. *Thamnochortus erectus* plants killed by fire had predominantly small and medium tussock diameters. *Thamnochortus insignis* plants killed by fire included the entire range of tussock diameters. Harvesting selectively killed small plants in both species.

Establishment after fire was exclusively by seed for *T. insignis* and by both resprouting from a subterranean base and from seed for *T. erectus*. Establishment after harvesting for both species was by both resprouting from a subterranean base and from seed. The study species did not have

similar frequencies of dead adults, resprouting adults and seedlings after harvesting or fire. Both species, also had different frequencies of dead adults, resprouting adults and seedlings after fire and harvesting.

Thamnochortus erectus rapidly produced culms after fire and both species rapidly produced culms after harvesting; the majority of which were unbranched unreproductive culms. *Thamnochortus erectus* produced significantly more culms per plant than *T. insignis*, although *T. insignis* produced more reproductive culms than *T. erectus*. The number of culms, and particularly the number of reproductive culms per *T. insignis* plant increased significantly between the first and second flowering season after harvesting, which was not the case for *T. erectus*. After fire, only *T. erectus* plants in the largest tussock diameter size class had > 25% reproductive culms per plant. *Thamnochortus insignis* had a significantly greater plant height than *T. erectus*, which may together with greater quantities of lighter seed give *T. insignis* a greater colonizing ability compared to *T. erectus*.

Resprouting plants of both species, independent of tussock diameter, produced culms from all over the tussock and from the edge of the tussock. Many individuals resprouting from the entire base, however, had the majority of culms at the edge of the tussock, suggesting that particularly for *T. erectus*, most dormant buds are peripheral.

This study provided evidence for massive *T. insignis* and low *T. erectus* seedling recruitment in the post-disturbance environment. The large increase in *T. insignis* seedling density after disturbance, and the concentration of seedlings in the "open" microhabitat indicate that the dormancy breaking cue for *T. insignis* is increased resources in the disturbed environment. Moreover, results suggest that germination is either directly or indirectly cued by fire, although post-fire recruitment was not confined to the first germination season after fire. Detailed germination studies are needed to verify this. In contrast, *T. erectus* seedling density was variable after disturbance and generally not much larger in the post-

disturbance environment compared to mature vegetation before disturbance, indicating that germination was not stimulated by environmental stimuli in the post-disturbance environment.

Results indicate that either after a fire or harvesting event, *T. insignis* pre-disturbance plant densities could easily be achieved despite high seedling mortality. In fact a disturbance event increases the successful establishment of the non-sprouter, *T. insignis*, largely by massive seedling recruitment. Population expansion of *T. erectus* after fire is probable, although not after harvesting. Population replacement was, however, possible after harvesting. This was largely due to the ability of the resprouter, *T. erectus*, to maintain population size by adult plant survival and vegetative growth after a disturbance event. *Thamnochortus insignis* can, thus, be seen as a pioneer species and *T. erectus* can be seen as persistent species.

4.2.3 PRACTICAL IMPLICATIONS

The fact that the persistent seed banks are not completely depleted, plant numbers are unaffected and seed production quickly returns to pre-disturbance levels after harvesting and fire, suggests that a disturbance event in any season would not adversely effect the populations of both species. Moreover, intense harvesting could be risked in the year preceding a planned burn for the non-sprouter, *T. insignis*. This is, however, not the case for the resprouter, *T. erectus*,as seedling recruitment is not increased after disturbance. Fire also reduces seed bank size, and this together with high pre- and post-dispersal seed losses following a harvesting event, result in a dramatic reduction in seed bank.size. It is also not known how long it will take surviving plants to accumulate sufficient reserves to withstand another disturbance event.

On the basis of the findings of this study (1 - 6) and observations of current management practices (7 - 11), the following recommendations for the sustainable utilization of the principle thatching reed species are made:

1) Only mature populations which have accumulated seed in their seed banks for several years (i.e. approximately ten years after a fire) should be harvested or burnt.*
2) The harvesting frequency should be approximately every five years, and never less than three years.*
3) A minimum fire frequency interval of seven years is suggested.*
4) The practice of harvesting populations at the time of seed dispersal or immediately afterwards, and before the season of new culms growth is recommended.
5) Harvested thatch should be removed to ensure maximum seedling recruitment.
6) Burning after seed dispersal and before the season of new culm growth is recommended.
7) The practice of not harvesting very small or inaccessible adult plants and occasionally leaving a few unharvested culms is recommended.
8) The practice of harvesting thatch with a mechanized brushcutter that aids in the dispersal of seed is recommended.
9) Care must be taken to prevent the trampling of seedlings by harvesters.
10) Harvesting methods should take plant recovery, especially for the non-sprouter *T. insignis*, into account and plants should not be harvested below the new culm growing tips.
11) High intensity fires which result in poor regeneration should be avoided.

Both *T. insignis* and *T. erectus* grow in habitats that are characterized by a high floristic and vegetational complexity (Section 1.3.1 and 1.3.2). Furthermore, these habitats contain many hundreds of localized endemics (Section 1.3.1 and 1.3.2). It is, thus, important that management practices are aimed at both the conservation of species biodiversity, as well as increased thatch production. With only thatch production as an objective,

*The time periods mentioned in 1, 2 and 3 above would potentially allow for seed bank accumulation and population replacement after disturbance.

managers of thatch stands use manangement practices, such as rotation burning outside the summer to early autumn period (Bond *et al.* 1984), elimination of shrub species or brushcutting entire stands (Ball 1991), that selectively suppress the growth of co-occurring overstorey (e.g. *Leucadendron* and *Proteaceae* species) and understorey (e.g. *Erica*, *Passerina* and *Metalasia* species) shrub species. This prevents inter-specific competition for limited resources and eventual suppression of thatch growth, decline in reproductive output, and local extinction (Cowling and Gxaba 1990). The danger exists that as a result of these types of management practices vegetation types with a high cover of thatch will become increasing disturbed, fragmented and species poor (Ball 1991). Both the goals of conservation of biodiversity and increased thatch production can, however, be achieved simultaneously by following a management guideline that includes a variable disturbance regime (i.e. varying the frequency and spatial extent of fires according to observed population levels) and such a management practice is recommended.

As interspecific competition is interrupted by recurring fires. Burning the veld on a rotation, after reproductive maturity (> 10 years) and before senescence of *Thamnochortus* plants (as senescence would result in the reduction of new seed production and consequent reduction in the pre-fire seed bank size) (*T. insignis*: < 20 years, *T. erectus*: < 80 years), and before the shrubs reach a size where they suppress *Thamnochortus* population expansion (< 10-15 years) is suggested. This management practice ensures both the conservation of co-occurring species (despite their suppression) and increased thatch production. Disturbance will regulate shrub overstorey density and the frequency of windows of reduced competition, allowing growth and expansion of understorey *Thamnochortus* species. Recovery of serotinous shrubs after fire will require a considerable time period (*ca.* 4-8 years to reach reproductive maturity) (Kruger and Bigalke 1984). Hence competitive effects on the understorey plants will be reduced, within this window after fire, relative to other times in the fire cycle. *Thamnochortus* populations are, thus, able to persist with co-occurring vegetation,

alternating between active and dormant phases, over many fire cycles, as long as the fire-free intervals do not exceed seed longevity.

For *Thamnochortus insignis*:

It is predicted that competition between seedlings of shrub and *T. insignis* species after fire reduces seedling survival of shrubs and limits their density (Kruger 1983, Bond 1987). *Thamnochortus insignis* plants also have a competitive advantage, because they have an extremely large reproductive output and persistent soil-stored seed bank. A planned late summer or autumn burn would ensure maximum regeneration of fynbos species, including *T. insignis* (Bond *et al.* 1984) and ensure conservation of species biodiversity. Burning outside the late summer to autumn period would result in the local extinction of the majority of fynbos species (Bond *et al.* 1984), although *T. insignis* with its persistent seed bank would show good regeneration provided that sufficient time has been allowed for soil seed bank accumulation. Prescribed burning in this season is not recommended if species conservation is an objective, although it could be used as a management tool to control shrub densities. Thatch plants can be harvested on a rotation when biomass levels have increased sufficiently. Prescribed burning could also be risked after harvesting *T. insignis* plants, provided that sufficient time has been allowed for seed bank accumulation (see previous discussion).

For *Thamnochortus erectus*:

In the case of *T. erectus*, fire would result in the rapid regrowth of the resprouter adults which occupy space and, thus, exclude both inter- and post-fire seedling regeneration of other species (Grubb 1977, Keeley 1977, Specht 1981, Kruger 1983, Keeley 1986). *Thamnochortus* plants may reproduce in several seasons within the duration of the window, producing a store of dormant long-lived seeds (Section 2.6). As *T. erectus* is longer lived than *T. insignis* the period between prescribed burns can be longer for this species. Non-sprouting shrubs are usually shorter lived than *T. erectus* and, thus, shrub seed is not always abundant after long inter-fire periods (i.e. >

20 years). Fire in these years would eliminate co-occurring shrubs, although not *T. erectus* plants and this practice is not recommended if species conservation is an objective,. although it could be used as a management tool to control shrub densities. Very long interval fires (> 50 years) are to be avoided as they would result in *Thamnochortus* plants undergoing density dependent mortality. Moreover, *T. erectus* plants may experience high adult mortality during intense fires which follow (Gill 1981), thus, leaving gaps for seedling recruitment. Should there be large numbers of shrub seedlings , these are generally more drought resistant, grow faster and, thus, there is a danger that they would outcompete *T. erectus* seedlings (Keeley and Zedler 1978, Parker 1984). This may result in reduced recruitment after the following fire, causing an overall decline in *Thamnochortus* populations (Keith and Bradstock 1994). Prescribed burning should not be risked immediately after harvesting *T. erectus* plants, as fire does not maximize recruitment in the species and adult plants may not be able to survive successive disturbance events. (Section 2.6). A few years should be allowed after harvesting to allow for adult plant recovery and soil seed bank accumulation. Prescribed burning should also not be risked in the growth season as this may result in poor regeneration of *T. erectus* plants (Section 3.6).

4.3 LIMITATIONS AND SUGGESTIONS

The major weakness of the study was that it was conducted at one study site for each species, and that it included only one disturbance event. Although prohibitive in terms of financial costs and time, an increase in the number of study sites for each species and the sampling of a number of differently aged populations would have increased the generality of the results. Seed bank studies should ideally be continued for more than two years, as seed production, seed predation and other factors are variable, and may effect seed bank sizes and dynamics (Lamont 1985, Auld 1987, Keeley 1987, Pierce 1990). An attempt was made to control variation in microhabitat factors between study sites.

Seedling density following disturbance is characteristically variable because of localized differences in conditions during the fire, pre-disturbance adult plant densities, season of the disturbance and post-disturbance climatic conditions (Keeley and Keeley 1981, Kruger 1983, Bond *et al.* 1984, Christensen 1985, Cowling 1987, Parker 1987). Actual experimental burning of populations may be the only way of adequately addressing how recruitment in the two study species varies with plant age since the last fire, fire season, fire intensity and post-fire climatic conditions. Seedling data should have ideally been collected at more frequent intervals and over a longer time period following fire and harvesting. Detailed germination studies need to be conducted on both species to elucidate the exact mechanisms of seed dormancy breaking.

The large variation in the data, as is the case with most seed bank studies, also limits its value. Sampling of soil seed banks was already more thorough in this study than in most other seed bank studies, and further sampling to reduce variance was not practical. Estimates of seed losses following burial from the seed bank study and the burial experiment are conflicting and there is no obvious explanation other than those given in the preceding discussion. Results from the "seed budget" must be viewed with some degree of caution for the above reasons. Generally, however, it was felt that trends were obvious and conclusions reached were well founded.

Several questions regarding the reproductive ecology, and especially the seed bank dynamics of *T. insignis* and *T. erectus* remain unanswered. Long term seed burial experiments with frequent evaluation of seeds would increase our understanding of the long term persistence of seeds in the soil. Special emphasis needs to be placed on the role of the microhabitat in influencing vegetation processes. Seed density and survival as well as seedling recruitment and survival needs to be experimentally determined for the different microhabitats. The extent to which spatial and temporal heterogeneity in the study site influences seed bank dynamics needs to be investigated. Field as well as laboratory germination studies on different

aged seed collected from both the plants and soil seed banks would shed light on the exact germination requirements of both species. Seedling mortality should be experimentally monitored at regular intervals to gain an understanding of the factors responsible for seedling death. Pollination biology of the two study species is also unknown. Seed viability studies of soil-stored seed would also be useful. An investigation into the pre- and post-fire seed bank dynamics would be particularly useful to gain a further understanding of the basic biology of the two species, as would the effect of different fire intensities and seasons.

Compared with other seed bank studies undertaken in the fynbos, this study has attempted to provided the most accurate representation of the seed bank dynamics of the study species by using a large number of samples and the simultaneous use of a number methods for estimating seed bank size and seed persistence/loss.

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APPENDIX A: BIOMASS ALLOCATION

5.1 INTRODUCTION

Biomass allocation in the two study species, *Thamnochortus insignis* and *Thamnochortus erectus*, was investigated. The following questions were addressed: (1) *How do each of the study species allocate biomass to the different plant parts?* (2) *Can the different plant life-histories explain these different patterns of biomass allocation?*

5.2 METHODS AND MATERIALS

Twenty whole *T. insignis* and *T. erectus* adult plants were randomly collected from the two study sites (Section 1.3), taking care to ensure that all root material was excavated. The dry weight of the plant parts were calculated using the method described by MacKey and Neal (1993). Plants were washed down with tap water and all soil and foreign plant material removed. The plants were given a final wash with distilled water, and laid out in a greenhouse on absorbant paper towel for a few hours and excess moisture was allowed to evaporate. Plants were then separated into the following categories: roots, base, culms and inflorescences. Material for each category was placed in a labelled brown paper bag and dried on wire shelves in a Memmert (Model 500) oven at 80°C for 48 hours. The contribution each category made up of the total plant dry weight (in grams) was determined after the plants had cooled to room temperature, using a Mettler AE 240 Dual Range Analytical Balance. Dried plants were handled with forceps to prevent any moisture from the hands affecting the final recorded weight. Total plant dry weight for above-ground plant parts (culms and inflorescences) and below-ground plant parts (roots and base) was calculated.

5.3 RESULTS AND DISCUSSION

Average total biomass in grams (x ± S.D., n = 20) was 153.88 ± 199.39 for *T. insignis* and 72.86 ± 76.70 for *T. erectus*. The difference in biomass between the two species was 2.11 times. Average above-ground biomass (x ± S.D., n = 20) was 118.84 ± 105.22 for *T. insignis* and 53.08 ± 58.45 for *T. erectus*. The difference in biomass between the two species was 2.24 times. Average below-ground biomass (x ± S.D., n = 20) was 35.04 ± 23.42 for *T. insignis* and 19.78 ± 18.71 for *T. erectus*. The difference in biomass between the two species was 1.77 times.

The results of this study are not consistent with the findings of Pate *et al.* (1991) who found substantial differences in above and below-ground biomass between 82 resprouting and non-resprouting species of south-western Australian Restionaceae. Mean culm (i.e. above-ground plant parts) : rhizome (i.e. below-ground plant parts) dry weight ratios, calculated by Pate and co-workers were 12.3 for non-sprouters and 2.9 for resprouters. Similar findings for other Australian species have been reported by Bowen and Pate (1993) and Pate and co-workers (1990). This study indicated that both species have high biomass allocation to above-ground plant parts (> 70%), with the non-sprouter, *T. insignis*, having slightly higher biomass allocated to this category than the resprouter, *T. erectus* (Table 5.1 and Figure 5.1). Biomass allocation to the below-ground plant parts was relatively small (< 28%) for both species, with the resprouter having slightly more biomass allocated to this category than the non-sprouter (Table 5.1 and Figure 5.1). Mean above-ground : below-ground dry weight ratios for both the non-sprouter species (3.39) and the resprouter species (2.68) in this study were similar to that of Pate and co-worker's estimates for resprouters. This indicates that the non-sprouter, *T. insignis*, allocates more biomass to below-ground structures than it's Australian counterparts do. It is not known whether *T. insignis* has a greater resprouting ability after deculming (i.e. harvesting) or grazing compared to non-sprouting Australian Restionaceae. *Thamnochortus erectus* allocates a lower percentage of the

total biomass to inflorescences (reproductive structures) and a higher percentage of the total biomass to roots than *T. insignis* (Table 5.1 and Figure 5.1). This is consistent with the findings of many studies which found greater reproductive effort in non-sprouter species compared to closely related resprouter species (Wells 1969, Hansen *et al.* 1991, Meney *et al.* 1994). Both species showed similar proportions of biomass allocations to the culms and tussock base (Table 5.1 and Figure 5.1).

Table 5.1. Estimated *T. insignis* and *T. erectus* biomass allocation. Data are average biomass allocation (dry weight in g) (mean ± standard deviation) to the different plant parts, namely below-ground (roots and base) and above-ground (culms and inflorescences) plant parts. Proportions (%) of biomass allocation with respect to the average biomass recorded in each category are displayed (n = 20 adult plants). Plants were collected at Zoetendalsvallei and at Zeekoeivlei (on the Agulhas Plain).

Plant part	Species	
	T. insignis	T. erectus
	Mean ± S.D (%)	Mean ± S.D (%)
Below ground		
Roots	9.30 ± 4.67 (6.04)	8.00 ± 8.23 (10.98)
Base	25.74 ± 20.39 (16.73)	11.78 ± 10.73 (16.17)
Total	35.04 ± 23.42 (22.77)	19.78 ± 18.71 (27.15)
Above ground		
Culms	113.49 ± 101.29 (73.75)	52.82 ± 58.16 (72.50)
Inflorescences	5.35 ± 5.28 (3.48)	0.26 ± 0.41 (0.35)
Total	118.84 ± 105.22 (77.22)	53.08 ± 58.45 (72.85)
Grand total	153.88 ± 119.39 (100)	72.86 ± 76.70 (100)

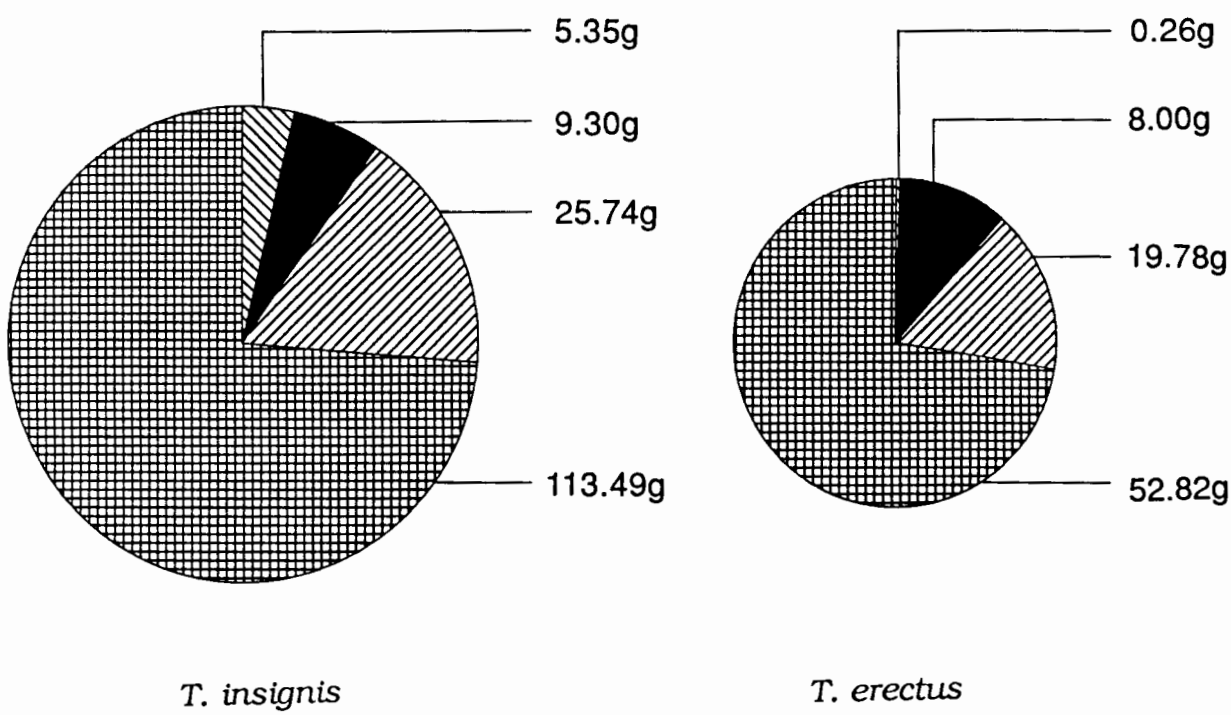

Figure 5.1. Pie diagrams of percentage biomass allocation (dry weight in g) to the different plant parts, namely below-ground (roots ■ and base ▨) and above-ground (culms ▦ and inflorescences ▨) plant parts, for a) *T. insignis* and b) *T. erectus*. Average biomass recorded in each category are displayed (n = 20 adult plants). Plants were collected at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

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APPENDIX B: SOIL TEMPERATURES

6.1 INTRODUCTION

Increased temperature fluctuations in bare soil after fire has been proposed as a method of breaking dormancy of seeds in fire-prone environments (Thompson *et al.* 1972, Brits 1986, Brits and Brown 1991, Pierce and Moll 1994). Harvesting also removes the insulating effects of vegetation cover which may also result in increased soil temperature fluctuations. Germination of seeds in both species is observed after the onset of the annual rains and cooler temperatures in winter and autumn in the upper layer of soil (Section 2.5.8). "Open" areas between fynbos vegetation appears to be the favoured microhabitat for seed germination or seedling survival of both species in mature vegetation (Section 2.5.8). Moreover, harvesting appears to promote seed germination or seedling survival, especially for *T. insignis*, possibly due to the creation of larger "open" areas (Section 2.5.8) (Singleton 1991). It was, thus, intended that as a result of these observations, the fluctuation of soil temperatures under the fynbos canopy and in bare soil in unharvested and harvested areas be measured for use in germination of seeds of both species in a controlled environment chamber. The study addressed the following questions: (1) *Does harvesting result in greater diurnal temperature fluctuations in the upper soil layer?* (2) *If so, are there differences between the different microhabitats, namely "open" areas and under fynbos canopy?* (3) *How do these differences change with soil depth?*

6.2 METHODS AND MATERIALS

Soil temperatures were measured in adjacent harvested and unharvested areas (i.e. Area 1 and Area 2 in 1993) at both study sites (Section 1.3). Measurements were made shortly before dawn and at midday in early winter and early summer, and autumn and early summer for *T. insignis and T. erectus*, respectively. The winter/autumn measurements were made as

these were the germination periods of the two study species. Early summer measurements were made to give an indication of the conditions experienced in the first summer after germination. Measurements were made on clear sunny days. A hand held thermometer was used to measure temperatures in shallow (0-1 cm) and in deep (3-4 cm) soils, both under the fynbos canopy and in "open" patches between plants. Six replicates of each measurement were made.

Three-way analysis of variance (ANOVA Type 1) (Zar 1984) was performed on daily temperature fluctuations of the soil (n = 6) in order to determine the influence of harvesting treatment, depth and vegetation cover. Each species was analysed separately, for both data collection periods. The statistical computer programme, Statgraphics 6.0 (STSC Inc.) was used (Statgraphics 1987). Temperatures measured in harvested and unharvested vegetation showed similar trends for microhabitat and soil depth, therefore, only temperatures measured in harvested vegetation are displayed.

6.3 RESULTS AND DISCUSSION

For both species, diurnal temperature fluctuations were higher in "open" patches than under fynbos vegetation. For *T. insignis*, the recorded temperatures were highly significantly different both in winter ($F = 112.685$, $P < 0.001$) (Table 6.1 and Table 6.2) and in summer ($F = 538.826$, $P < 0.001$) (Table 6.1 and Table 6.2). For *T. erectus*, the recorded temperatures were highly significantly different both in autumn ($F = 33.109$, $P < 0.001$) (Table 6.1 and Table 6.2) and in summer ($F = 73.606$, $P < 0.001$) (Table 6.1 and Table 6.2). For both species, diurnal temperature fluctuations were higher in shallow (0-1 cm) than deep (3-4 cm) soil depths. For *T. insignis*, the recorded temperatures were highly significantly different both in winter ($F = 112.685$, $P < 0.001$) (Table 6.1 and Table 6.2) and in summer ($F = 296.607$, $P < 0.001$) (Table 6.1 and Table 6.2). For *T. erectus*, the recorded temperatures were highly significantly different both in autumn ($F = 111.083$, $P < 0.001$) (Table 6.1 and Table 6.2) and in summer ($F = 32.343$, P

< 0.001) (Table 6.1 and Table 6.2). For both species, diurnal temperature fluctuations were slightly higher in the harvested than in unharvested areas. For *T. insignis*, the recorded temperatures were highly significantly different in winter ($F = 63.794$, $P < 0.001$) (Table 5.3) and not significantly different in summer ($F = 0.164$) (Table 6.2). For *T. erectus*, the recorded temperatures were significantly different in summer ($F = 5.901$, $P < 0.05$) (Table 6.2) and not significantly different in autumn ($F = 0.970$) (Table 6.2).

For *T. insignis* in summer, the interaction between vegetation cover and harvesting treatment ($F = 44.088$, $P < 0.001$) (Table 6.2) and soil depth and harvesting treatment ($F = 45.561$, $P < 0.001$) (Table 6.2) were significant. For *T. insignis* in summer, the interaction between soil depth and vegetation cover ($F = 0.169$) (Table 6.2), and vegetation cover and soil depth and harvesting treatment ($F = 1.262$) (Table 6.2) were non-significant. For *T. insignis* in winter, the interaction between vegetation cover and soil depth was significant ($F = 71.489$, $P < 0.001$) (Table 6.2). For *T. insignis* in winter, the interaction between vegetation cover and harvesting treatment ($F = 0.351$) (Table 6.2), soil depth and harvesting treatment ($F = 1.800$) (Table 6.2), and vegetation cover and soil depth and harvesting treatment ($F = 0$) (Table 6.2) were non-significant.

For *T. erectus* in summer, the interactions between vegetation cover and soil depth ($F = 0.362$) (Table 6.2), harvesting treatment and vegetation cover ($F = 0.015$) (Table 6.2), harvesting treatment and soil depth ($F = 2.091$) (Table 6.2), vegetation cover and soil depth and harvesting treatment ($F = 0.209$) (Table 6.2) were non-significant. For *T. erectus* in autumn, the interaction between vegetation cover and harvesting treatment ($F = 22.206$, $P < 0.001$) (Table 6.2), and soil depth and vegetation cover ($F = 5.843$, $P < 0.05$) (Table 6.2) were significant. For *T. erectus* in autumn, the interaction between soil depth and harvesting treatment ($F = 0.280$) (Table 6.2), and vegetation cover and soil depth and harvesting treatment ($F = 0.649$) (Table 6.2) were non-significant.

Seedling density of both study species, but especially *T. insignis*, was greatest in environments which experience the largest diurnal temperature fluctuations (Section 2.5.8), namely "open" areas, shallow soils and harvested vegetation. From these results it does appear that increased temperature fluctuations of exposed soil during autumn months break dormancy of seeds of both study species. The cue of alternating temperatures in autumn is known to be of importance for the germination of a number of fynbos species (Brits 1986, Brits and Brown 1991, Pierce and Moll 1994) The temperature settings of the controlled environment chamber for the seedling emergence experiment was set accordingly to obtain maximum germination and seedling emergence. Detailed germination studies are, however, needed to verify whether increased diurnal temperature fluctuations or another environmental stimulus associated with "open" areas (e.g. increased light or changes in the spectral composition), break seed dormancy in both species.

In a similar study by Kilian (1991) in dune fynbos, "open" patches in mature vegetation had temperature fluctuations closer to those in the burnt area than those under the fynbos canopy. Soil temperatures were not measured for burnt areas in this study. However, similar soil temperatures were obtained in harvested and unharvested vegetation, especially for "open" areas. This indicates that seed and seedlings in mature *Thamnochortus* vegetation experience similar soil temperatures to harvested vegetation. This is probably due to the "openness" of the vegetation type compared to other fynbos vegetation types. I predict that the soil temperatures experienced in harvested and unharvested vegetation will become increasingly different with increasing vegetation age (i.e. as the canopy becomes more "closed"). Kilian (1991) also found that fluctuations were larger at the 0-1 cm soil depth than at the 3-4 cm soil depth.

A major fault of this study is that data were only collected over one day for each species, in each of the two seasons, due to severe time constraints. As a result, the generality of the results is uncertain.

Table 6.2. Three-way analysis of variance on the effects of harvesting treatment, depth and vegetation cover on daily temperature fluctuation. Data for the *T. insignis* site are for the a) winter and b) summer data collection periods. Data for the *T. erectus* site are for the a) autumn and b) summer data collection periods. N.S. = non-significant.

		T. insignis				T. erectus			
		a) Winter		b) Summer		a) Autumn		b) Summer	
Source of variation	df	F	P	F	P	F	P	F	P
Harvesting treatment	1	63.79	< 0.001	0.16	N.S.	0.97	N.S.	5.90	< 0.05
Depth	1	296.61	< 0.001	112.69	< 0.001	111.08	N.S.	32.34	< 0.001
Vegetation cover	1	538.83	< 0.001	112.69	< 0.001	33.11	N.S.	73.61	< 0.001
Interactions:									
Harvesting treatment x Depth	1	1.80	N.S.	45.56	< 0.001	0.28	N.S.	2.09	N.S.
Harvesting treatment x Vegetation cover	1	0.35	N.S.	44.09	< 0.001	11.21	N.S.	0.02	N.S.
Depth x Vegetation cover	1	71.49	< 0.001	0.17	N.S.	5.84	< 0.05	0.36	N.S.
Harvesting treatment x Depth x Vegetation cover	1	0.00	N.S.	1.26	N.S.	0.65	N.S.	0.21	N.S.

Table 6.1. Minimum, maximum and diurnal fluctuation of soil temperatures at two soil depths. Data are average (mean ± standard deviation) soil temperatures (°C) for a) winter (*T. insignis*) / autumn (*T. erectus*) and b) summer at two soil depths, namely shallow (0-1 cm) and deep (3-4 cm) in harvested vegetation (i.e. Area 1) (n = 6 temperature readings per treatment). Data were collected at Zoetendalsvallei and Zeekoeivlei (on the Agulhas Plain).

Season		Species															
		T. insignis								T. erectus							
		Time															
		Pre-dawn			Midday			Temperature fluc.		Predawn			Midday			Temperature fluc.	
	Depth	Mean	S.D.	Min.	Mean	S.D.	Max.	Mean	S.D.	Mean	S.D.	Min.	Mean	S.D.	Max.	Mean	S.D.
a) Winter										a) Autumn							
Soil cover																	
Open patch	Shallow	6.22	0.90	5.00	24.45	1.39	27.00	18.23	0.92	8.07	0.80	7.00	30.13	3.11	34.00	22.07	2.61
	Deep	9.25	0.50	9.00	19.93	1.33	21.90	10.68	1.01	10.05	1.64	7.00	26.17	0.76	27.00	16.12	1.35
Under canopy	Shallow	6.97	0.59	6.30	16.58	0.96	18.10	9.62	0.69	9.50	0.99	8.00	25.38	1.33	27.00	15.88	1.16
	Deep	9.20	0.69	8.20	16.12	0.80	17.50	6.92	0.8	10.13	0.85	9.00	21.72	1.11	23.00	11.58	0.66
b) Summer																	
Soil cover																	
Open patch	Shallow	13.92	1.19	12.60	37.47	1.52	40.00	23.55	1.58	14.95	1.08	14.00	40.38	3.53	44.00	25.43	2.59
	Deep	15.05	1.39	12.90	35.58	1.68	37.00	20.53	2.77	16.27	2.05	13.70	35.90	1.62	38.10	19.63	2.16
Under canopy	Shallow	14.63	0.38	14.00	26.55	1.87	29.00	11.92	1.53	14.78	1.11	13.50	28.52	1.60	30.30	13.73	1.78
	Deep	15.27	0.41	15.00	25.08	3.12	28.90	9.82	3.32	15.92	0.66	14.90	24.23	2.85	28.00	8.32	3.08

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APPENDIX C: SEEDLING GROWTH RATES

7.1 INTRODUCTION

Thamnochortus insignis and *T. erectus* seedling growth rates were measured in a controlled environment chamber for 50 days after seedling emergence. The study addressed the following question: (1) *Do the two species have different seedling growth rates?*

7.2 METHODS AND MATERIALS

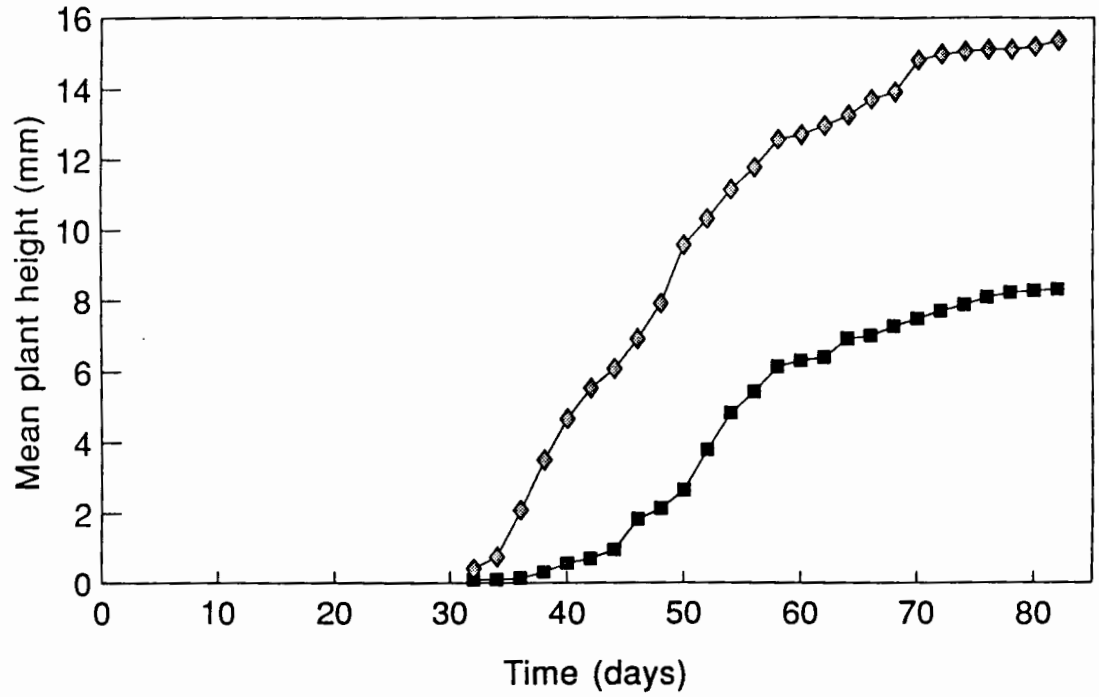
Seeds of both species were germinated in soil cores laid out on soil-filled pots in a controlled environment chamber (Section 2.4.6 and 2.4.6.3). The height (from the level of the soil surface to the tallest culm) of all emergent seedlings (*T. insignis* 1992: n = 24 and 1993: n = 23; *T. erectus* 1992: n = 19 and 1993: n = 17) were measured every second day for 50 days after seedling emergence. *Thamnochortus insignis* seeds were collected from the study site, Zoetendalsvallei, and *T. erectus* seeds were collected from the study site, Zeekoeivlei (Section 1.3).

7.3 RESULTS AND DISCUSSION

Seedlings of both species emerged from the soil after 32 days of incubation at temperature and light conditions typical of autumn/winter in the south-western Cape (Section 6.3, Kilian 1991). Both species show a rapid initial mean growth rate (i.e. seedling height gain with time), which slows down after 38 days following emergence for *T. insignis* and after 40 days following emergence for *T. erectus* (Figure 7.1). The growth increase was greatest for *T. insignis* (1992) and slowest for *T. insignis* (1993), and intermediate for *T. erectus* (1992 and 1993) (Figure 7.1). Mean seedling growth rate was dissimilar for *T. insignis* seedlings germinated from seed collected in 1992 and 1993 (Figure 7.1). Mean seedling growth rate was similar for *T. erectus* seedlings germinated from seed collected in 1992 and 1993 (Figure 7.1).

From the results of this study, both species appear to grow rapidly under the light, moisture and temperature conditions present in the controlled enviroment chamber for the duration of the experiment (Section 2.4.6 and 2.4.6.3). It is, however, unlikely that similar growth rates will be achieved by both species in the field.

a) *T. insignis*



b) *T. erectus*

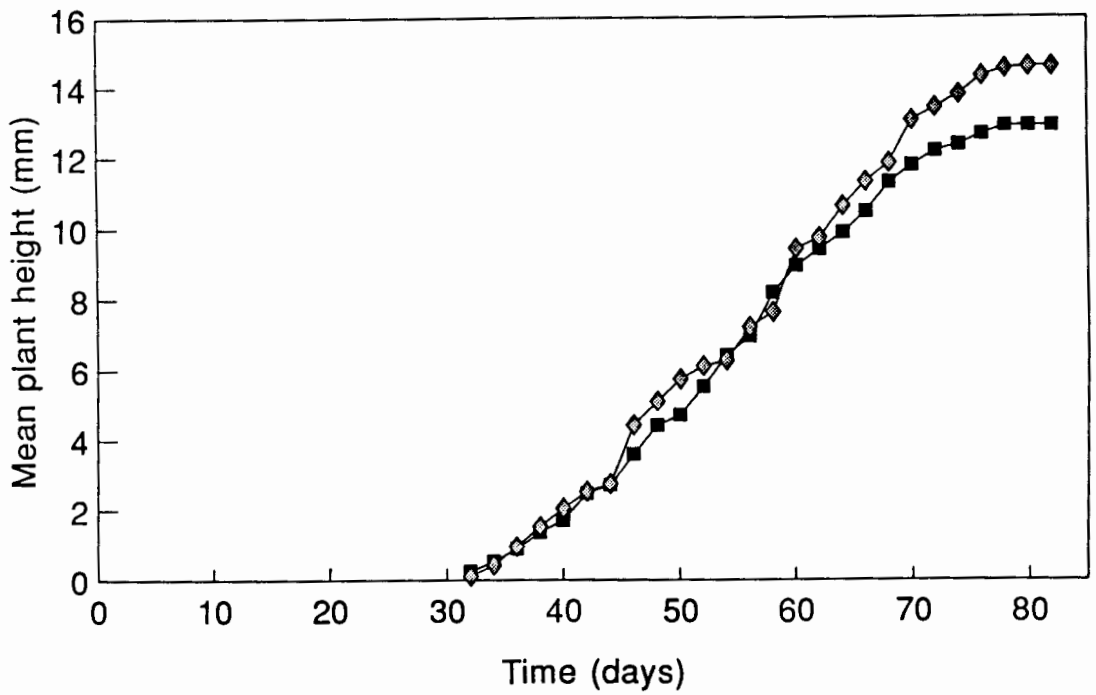


Figure 7.1. Growth rates for a) *T. insignis* (1992 ◆ ; 1993 ■) and b) *T. erectus* (1992 ◆ ; 1993 ■) seedlings grown in a controlled environment chamber (alternating 20°C/10°C for 10/14 h light/dark, relative humidity 50% day and 65% night). Seedling height (mm) was measured every two days for 50 consecutive days following emergence.

7.4 REFERENCES

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